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THE LIFE OF THE MOLLUSCA

UNIFORM WITH THIS VOLUME

THE LIFE OF CRUSTACEA

BRITISH FRESHWATER FISHES

THE OX AND ITS KINDRED

THE SNAKES OF EUROPE

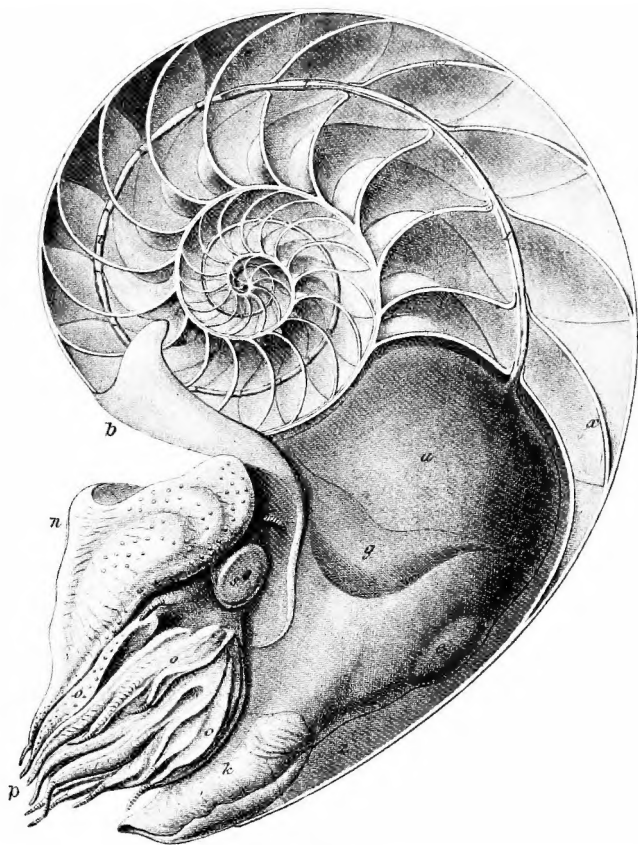


PLATE I

The Pearly Nautilus (*Nautilus pompilius*, Linn., after Owen). The chambered shell has been laid open down to the central plane.

- a. The mantle.
- b. The dorsal fold of the mantle.
- e. Nidamental gland.
- g. Shell muscle.
- i, i, i. Shell siphuncle.
- k. Funnel.

- n. Hood
- o, o, o. Pedal lobes.
- p. Tentacles.
- s. Eye.
- x, x. Septa.
- z. Body chamber.

THE LIFE OF THE MOLLUSCA

BY

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OF THE BRITISH MUSEUM (NATURAL HISTORY)

PAST-PRESIDENT OF THE MALACOLOGICAL SOCIETY OF LONDON

WITH THIRTY-TWO PLATES AND A MAP

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PREFACE

THE object of the present work is to give a succinct account of what is known concerning the life of that branch of the animal kingdom to which the Snail, the Oyster, and the Cuttlefish belong—the MOLLUSCA.

Especial attention has, therefore, been given to their history, relationships, and everyday life (ecology), with only general notes on their anatomy, classification and distribution, etc.

The numerous illustrations it is hoped will prove helpful to students. Many figures have been specially drawn by Miss G. M. Woodward, but most of them first appeared in the late Dr. S. P. Woodward's "Manual of the Mollusca," the original drawings and engravings for which are in the possession of the writer. Cordial thanks are due to the Trustees of the British Museum for their courteous permission

to reproduce illustrations from their publications or taken from specimens on exhibition in the Natural History Museum. Other illustrations have been kindly lent by Mr. W. M. Webb, F.L.S.

To his colleagues in the Natural History Museum, Mr. E. A. Smith, I.S.O., and Mr. G. C. Crick, the author is indebted for valuable assistance in regard to points of nomenclature.

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*All the Plates (except Plate I., frontispiece) and the Map are at the
end of the book.*

THE LIFE OF THE MOLLUSCA

CHAPTER I

GENERAL INTRODUCTORY

SHELLS have ever been attractive objects owing to the beauty of form and coloration displayed by so many of them, and though they are no longer fashionable objects to collect, every one in his, or her, young days has listened with wonder to the supposed roar of the sea in their cavities, while there are some few who retain their predilection for them throughout life, and make more or less extensive collections. Fewer persons still, however, pay any attention to the animal that formed and built the shell, for it has never stood high in popular estimation; indeed, unless good to eat, it is usually an object of aversion, and yet there is no group of the invertebrate, or backboneless animals, that better repays study.

The Mollusca (soft-bodied animals), of which the Slugs and Snails, the Oysters and the Cuttlefishes,

are familiar examples, as now restricted, form a well-marked group (subkingdom or phylum) of the animal kingdom.

Owing to their plasticity, they differ very much among themselves in external form ; indeed, some of the more aberrant members are at first scarcely recognizable as molluscs at all ; nevertheless, apart from the protective shell, which is a leading feature of the group, a remarkable uniformity characterizes their internal organization in its main features, especially in the young forms.

Externally most possess a "head" ; a ventral creeping organ, the "foot" ; and a dorsal covering, the "mantle," which bears and secretes the shell. This shell forms a protection to the more vital organs, and into it the animal can generally withdraw for security from attack.

The mantle does not usually reach far beyond the shell-margin when the animal is extended, but in some cases it curls round over the shell (Plate II., Fig. 2), and even, as in the Cowry (*Cypræa*), meets on the top (Plate II., Fig. 9). In the more specialized Mollusca there is a tendency to the reduction, even to disappearance, of the shell, and in these there is a corresponding liability for the shell to become more and more enveloped permanently in the mantle as the animal becomes less and less able to use it as a place of retreat (see *infra*, p. 105).

The muscular foot, which is generally an organ of

locomotion, takes various forms in the different groups of Mollusca; the Univalves (Snails and Whelks) creep along by its means; the Bivalves employ it to burrow with; in the Cuttlefish it is drawn out into the "arms"; in other Mollusca it is transformed into fins to swim with; whilst in some, like the Oyster, it has ceased to be used, and has degenerated into a mere rudiment. Most of the muscles of the body are concerned with the extension or retraction of the different organs of the body, and do not call for special enumeration.

The shell is mainly composed of carbonate of lime, as much as 95 per cent., in the form of calcite or arragonite, being often present, with the admixture of a chitinous substance, "conchyolin"; a little phosphate of lime and a trace of carbonate of magnesium are also present. It originates in a shell-gland, or pit, in the embryo, and the successive layers of which it is built up (Plate VII., Figs. 11 and 12) are formed as the animal grows by additions to the margin, and are deposited in order from the outermost to the inner one by a series of special cells situated in the thickened margin of the mantle. The outermost layer, or "periostracum,"* contains the greatest abundance of chitine-like material in its composition, and is the work of the cells at the very

* The term "epidermis," which has been extensively misapplied to this layer, should be reserved exclusively for the outer layer of the skin of the animal itself.

edge of the mantle. Its function is to protect the underlying layers from the action of acid in the water, or from that of the weather on land. It varies greatly in appearance, being sometimes smooth and shiny, at others, rough and coarse; frequently it is fibrous (Plate XXVIII., Fig. 2*a*). In many forms it readily rubs off; in others it is firmly united to the true shell beneath. The second, or principal layer, usually forms the greater thickness of the shell proper, or "ostracum," and is secreted by cells farther from the mantle margin; it may be coloured, and is often made up of prisms of calcite, as in *Pinna*, though it frequently has a porcellaneous structure. The cells more remote from the mantle edge deposit the innermost layer of the ostracum, thus thickening and strengthening the shell. This layer ("nacreous layer") is of arragonite, and frequently formed with overlapping plates, thus giving rise to the iridescent appearance known as Mother-of-Pearl. The remaining surface of the mantle also secretes shelly matter on occasion, either for the purpose of further strengthening the shell, of repairing an injury remote from the edge, or of filling up unoccupied spaces (Plate VII., Fig. 13); and in most Mollusca this deposit differs in structure from that of the other layers.* In the pearl-producing shells, how-

* The term "hypostracum" has been applied to the shelly layers immediately under the points of attachment of the muscles that secure the animal to the shell, but they do not

ever, such as the Top Shells (Turbinidæ and Trochidæ), the Pearl Oyster (*Meleagrina*), and many freshwater Mussels (*Unio*, *Anodonta*, etc.), as well as *Nautilus*, this last form of shelly secretion is not differentiated from the nacreous layer, and is very abundant. In the case of the Pearl Oyster and freshwater Mussels, foreign bodies introduced accidentally or intentionally between the mantle of the animal and the shell become coated with pearl. In this way "blister pearls," and occasionally detached pearls, are formed; but the true pearl of commerce, as will be shown later (*infra*, p. 79), is developed within the tissues of the animal.

The successive additions along the growing edge of the shell generally leave ridges or marks parallel with it, that are known as "lines of growth." The deposition of shell does not go on continuously; every now and again there comes a period of rest, and these rest periods are frequently indicated by the occurrence of a stronger ridge or mark. The different details of sculpturing on the surface of the shell—striæ, ribs, spines, etc.—are all the products of corresponding irregularities on the margin of the mantle, and were, when first formed, situated on the growing edge. Certain molluscs, especially among the Gastropoda, further possess the power of dissolving and removing portions of their shells, either

appear to differ in microscopic structure from the shell immediately beneath them.

from the exterior or from the interior, as occasion may require.

The lime for the shell being probably obtained by the animal mainly from its food, it follows, especially in the case of the vegetable feeders, that where lime is abundant in the soil or water, and consequently in the plant tissues, the shell tends to become abnormally thick and heavy; while other members of the same species living where lime is scarce, will have exceedingly thin shells. The latter condition is very observable in the larger Land Snails of the Channel Islands, where, indeed, the living individuals will even resort to the shells of their dead comrades to obtain the requisite supply. Isolated cases of abnormally thick shells are probably due to physiological peculiarities of the individual, enabling it to absorb lime more easily than its fellows.

Internally the common trait in the Mollusca is the reduction of the coelum, or body cavity, to a space around the heart, and the concentration of the principal nerve centres ("ganglia") into a ring or collar surrounding the oesophagus.

All sections of the group, except the Bivalves, have a distinctive feeding organ called the "radula," and in their development almost always pass through what is known as the "veliger stage" (see *infra*, p. 93).

The heart, which is well developed, is entirely arterial—that is to say, only receives the blood after

it has been aërated in the gills, and distributes it over the body through the circulatory system. The latter is peculiar in that its channels are distended in places into wide spaces, or sinuses, which are insinuated among the various organs, and so diminish the body cavity.

The structure of the gills has been largely employed in the classification of the Mollusca. The gills, which are generally situated in a cavity under the mantle, vary in number from one in the majority of the Gastropoda to eighty pairs in some of the Chitons, or Coat-of-Mail Shells (Polyplacophora).

Each gill (or "ctenidium") consists of an axis containing two blood-vessels, one to bring the blood to the gill, the other to convey it away after it has been aërated in the respiratory filaments. Of these last there is a row on either side of the axis, each filament being more or less flattened. In order to obtain the greatest possible amount of surface exposed to the water for aëration, these filaments are either expanded into leaf-like plates (Aspidobranchiate, Plate III., Fig. 1), as in all the earlier representatives of each of the principal classes, or lengthened out (Pectinibranchiate, Plate III., Fig. 2). Further modifications are dealt with later on.

The nervous system of the Mollusca acquires peculiar importance in that, while every modification of an organ is reflected in it, it is the last feature to be influenced by these changes, and hence is of

extreme value in tracing relationships of the various parts. Its principal elements (Plate III., Fig. 3) comprise a series of paired nerve centres or ganglia; of these one pair, the "cerebral ganglia," lying above the œsophagus, sends off nerves to ("innervates") the head, eyes, and the special organs of sense; another pair, the "pedal ganglia," is situated below the œsophagus; whilst the "pleural ganglia," lying one on each side just above the pedal ganglia, form the third pair. These several ganglia are united by nerve cords, so that the whole forms a ring or collar round the throat. In the more primitive Mollusca the two last named are somewhat removed back from the other pair, but in the more specialized forms they are in proximity to it, and the resultant œsophageal ring is much more concentrated. Four nerve cords run back from either side of the ring, two in connection with the pedal ganglia serving the foot, and two in connection with the pleural ganglia innervating the viscera. These last, which are the more important, and are provided with minor nerve centres, are united towards their terminations, thus forming a continuous loop, known as the "visceral loop."

Various sense organs are present. Many of these are situated on the integument, and are probably, like the tentacles, organs of touch. Eyes are found in most forms, sometimes very perfect organs, as in the higher Cuttlefishes; in Snails generally they are

less well developed, and placed near the base of the "horns," or on the summit of a special pair. The Bivalves, being headless, have usually no eyes; but some possess them during their larval existence, and they persist in the adult Mytilidæ and *Pteria* (= *Avicula*). Secondary visual organs are developed in certain forms, and more usually occur in some part of the margin of the mantle or siphons (see *infra*, p. 133). In the case of one or two molluscs eyes are developed over the back.

That molluscs can hear is inferred, rather than known, from the presence of "otocysts," small cavities filled with fluid in which grains of shelly material float. These otocysts are situated close to the pedal ganglia, and supplied by nerves from the cephalic ganglia (Plate III., Fig. 3, o).

From their discrimination of food some Mollusca appear to be capable of tasting, and they certainly can smell. The seat of the olfactory sense is believed to vary, and in some to reside in a tentacle, while in others it can be traced to a special organ called the "osphradium," which in marine snails is situated close to the gills, and resembles them somewhat in appearance.

For procuring their food all classes of the Mollusca, except the Pelecypoda, are furnished with one or a pair of horny mandibles or jaws (Plate III., Figs. 4-8). and the special feeding organ, the radula (Plate III., Figs. 11-22).

The mandible is single, and placed on the upper side of the mouth in the Limpets (Patellidæ), one of the Sea-Slugs (*Ægives punctilucens*), the Land and Freshwater Snails (Pulmonata, Plate III., Figs. 5 and 6), and the Elephant's-Tusk Shells (Dentaliidæ). Two kinds of Pond Snails (*Limnæa* and *Planorbis*) have three mandibles, an upper and two side plates (Plate III., Fig. 7). The majority of the other gastropods—for the carnivorous species are generally without them—have two lateral plates. Many of these are ornamented with most elaborate patterns, and some have raised projections on them like a file (Plate III., Fig. 8).

The Cephalopoda also have a pair of mandibles, upper and lower, resembling a Parrot's beak, save that the upper fits within the lower one (Plate III., Fig. 4).

These mandibles are formed apparently of dense chitine, strengthened in the case of *Chætoderma* and *Nautilus* with carbonate of lime.

The radula is so important a feature as to call for more detailed mention. With its supporting cartilages and muscles it occupies the position in the mouth assumed by the tongue in the higher animals, and much resembles that organ in general appearance. The radula itself, however, consists of a series of recurved teeth formed of dense chitine, attached in transverse rows to a membrane of the same substance. In the Limpets (Docoglossa) the teeth

further contain as much as 27 per cent. of silica hydrate or opal in their composition, while in the rest of the Gastropoda the chitine is hardened superficially by deposits containing calcium, iron, and phosphoric acid, amounting in all from 2·4 to 6 per cent. The Chitons differ from this second group in alone having ferric oxide as the most important mineral constituent. In use, not only is the whole tongue-like mass protruded and worked with a licking action, but the radula moves backwards and forwards on its surface over the cartilages like a chain saw. The number of teeth in each transverse row varies from one, as in certain of the sea-slugs (*Æolis*, *Elysia*, etc.) and species of *Chætoderma*, to upwards of 200 or 300, as in the Top Shells and their allies (*Trochus*, *Haliotis*, etc.). When more than one is present the teeth generally vary in shape, but those on either side of the centre correspond each to each. The number of rows also varies from only a few to very many, so that in some Mollusca, like the Limpet, the radula is nearly twice as long as the animal.

In all, the teeth in front tend to become worn away by constant use, and to replace them fresh teeth are continually being formed at the other end, which is kept in a special sac or pouch under the gullet. The longest radulæ are generally found in those molluscs, like the Limpet, that feed on the microscopic plants growing on rocks, the teeth in

such case being more quickly worn away by use. The worn-out teeth usually fall off and are lost, but in one tribe (Ascoglossa = Elysioidea) they are received and retained in a special sac.

The total number of teeth in the radula consequently varies greatly in the different kinds. In some species of *Chætoderma* there is but a single tooth present, while the Whelk (Plate III., Figs. 16 and 17) has about 250, a big Limpet 2,000, the Periwinkle 3,500, the Common Garden Snail 15,000, and the big Grey Slug (*Limax maximus*) 26,800. In certain instances they almost baffle calculation, as many as 750,000 being computed for *Umbra-culum*.

Since each succeeding row of teeth resembles its predecessor, a longitudinal striped pattern results when the teeth in the transverse rows vary in shape and colour. In each row there is generally a central, or "rhachidian," tooth present, flanked on either side by "laterals." These laterals may be of one type, as in the Common Garden Snail and its allies (*Helix*), or they may be divisible into two or three sets, when those nearest the central tooth are styled "admedian" and the outer ones "marginal," these two series being generally divided by a conspicuous tooth, or "major lateral." This is expressed by formulæ, as 1 : 1 : 1 (Plate III., Figs. 16 and 17), 2 : 1 : 1 : 1 : 2 (Plate III., Fig. 15), and when the marginal teeth are very numerous, ∞ : 5 : 1 : 5 : ∞

(Plate III., Fig. 13), $\infty : 0 : \infty$ (Plate III., Fig. 14), etc.

The shapes of the teeth are so constant in the several molluscs that they assist not only in the determination of families and genera, but, with few exceptions, in that of species also.

The forms of the teeth are, further, some index to the diet of the animals, the purely herbivorous having short, broad-pointed teeth, the carnivorous sharp-pointed teeth, which in those feeding on living animals are barbed to retain their prey, while in the Cones the teeth are not only barbed, but perforated and connected with poison glands.

In habit the Mollusca are far from active, only some of the Cuttlefishes being capable of spasmodic rapid motion, so much so that the term "sluggish," borrowed from them, best describes them.

The exact relationship of the Mollusca is difficult to determine, though they belong to the same division of the animal kingdom as the Chætopoda, Gephyrea, Rotifera, Bryozoa, and Brachiopoda; but on the whole it is considered that the most archaic molluscs, the Chitons, come nearest to the free Polychetes, such as the gaudy Sea-Mouse (*Aphrodite*), so common on our coasts.

CHAPTER II

CLASSIFICATION

THE Mollusca are divisible into five principal groups or classes :

CLASS I.: The AMPHINEURA, of which the Chitons (Coat-of-Mail Shells) are the type.

In these the body is more or less elongate, without a distinct head, the foot forming the ventral surface. The extremities of the alimentary canal lie at either end of the body, and do not in any way approximate each other, while the various organs are situate in pairs on either side of the central axis, so that the two halves of the body correspond, and the animal is symmetrical.

This Class is divided into two orders, POLYPLACOPHORA and APLACOPHORA.

Order I. : POLYPLACOPHORA, the Coat-of-Mail Shells, or Chitons (Plate IX., Figs. 1-3 ; Radula Plate III., Fig. 11) are readily distinguished by being alone amongst the Mollusca in possessing a shelly covering of many pieces, called the "lorica."

There are eight plates or valves in all on the back of the animal, fitting one over the other like the tiles on a roof. Generally the lorica is surrounded by a leathery "girdle," so called, which helps to unite the several plates, and which, though sometimes naked, is usually studded with scales or beset with bristly spines.

In some forms the body is very long, and the shelly plates are placed at intervals. The muscular foot extends the whole length of the under surface of the body; the end of the snout is just visible; there are no tentacles. A row of small gills is seen along each side under the edge of the mantle. The valves are perforated for the passage of sense organs, which in the family Chitonidæ are in part converted into eyes. When detached from the rocks to which they cling, the animals will coil up after the fashion of the well-known Wood-Louse.

Order II. : The APLACOPHORA, or SOLENOGASTRA, are so modified that they scarcely resemble molluscs at all. The body is worm-like, and there is no trace of a shell, but the much thickened outer skin contains shelly spicules. The foot is extremely reduced, or altogether wanting. The gills are in a chamber at the latter end of the body, into which chamber also the excretory orifices open. Their blood is red. Two sub-orders are distinguished :

Sub-Order I : NEOMENIINA (Plate IX., Figs. 4 and 5), in which the foot is sunk in a groove along the

ventral side of the body. The radula is of the many-toothed order or wanting.

Sub-Order 2: CHÆTODERMATINA, represented by a single genus *Chatoderma* (Plate IX., Fig. 6), in which the body is extremely long and cylindrical; the foot is wanting, its position being merely indicated by a groove; whilst the radula is represented by a single tooth.

CLASS II.: The GASTROPODA (Plate II.), typified by the Snail and Whelk.

In these there is a distinct head, furnished with one or two pairs of contractile sense organs, the "tentacles," or "horns," the form of which varies greatly in different groups. The two eyes are situated on the tentacles (the hinder pair when four are present), and are generally carried on tubercles near the base, but they sometimes appear halfway up, while in the Common Snail and his kindred they are, as well known, borne aloft on the summits of the "horns."

The ventral foot forms a creeping disc, and surmounting it the visceral organs within the covering mantle are borne as a twisted hump, generally covered by a shell formed in a single piece. This shell is attached to the body by a powerful muscle, which serves to withdraw the animal into its house.

The torsion of the body is brought about by a double process (Plate IV., Fig. 1, A-D). Firstly, as

in the Cuttlefishes, the latter half of the alimentary canal is bent underneath the body till its termination approximates the mouth. Then the visceral mass is twisted round laterally, so that the terminal portion of the alimentary canal, with the two gills and other paired organs on either side of it, are brought round by the right side till they lie nearly over the head, and the original left gill and accompanying organs become in position the right-hand ones, while the visceral nerve loop is twisted into a figure of 8. Next, the original left (now right) gill and its accompanying organs tend to wither and eventually disappear. In some cases the secondary twist takes place in the reverse direction, or round by the left side, when a left-handed animal results, and the originally right gills, etc., are suppressed.

In this way the animal becomes asymmetrical, organs on one side of the body not being matched by corresponding ones on the other. A further result of the secondary, rotary twist is that the shell, which was beginning to coil forwards over the animal's head, or exogastrically, as it does in *Nautilus*, is swung round so that it coils backwards, or endogastrically.

The shell secreted by the mantle covering this twisted visceral hump, of course, reflects its form in every respect. Essentially the resultant shell is a longer or shorter hollow cone. In some, such as the adult Limpet, it is a simple cone, but in by far the greater number it is an elongated cone, coiled

round and round, each coil forming a "whorl," the last being the "body whorl" (Plate V., Figs. 1 to 10). This coil may be a flat one, but most Gastropods have the visceral dome and shell twisted dextrally—that is to say, when the shell is placed with the mouth uppermost, and the apex directed away from the observer, the mouth lies to the right hand of the axis of the shell. Some are wound in the opposite direction and are sinistral. Reversed varieties of animals and shells normally dextral, or normally sinistral, are often met with, as well as species in which the coiling of the animal and shell is indifferently dextral or sinistral in the individuals composing it. There are, moreover, Gastropods whose shells coiled in one direction enclose animals whose organization is that usually associated with shells having the opposite twist. Thus among the Ampullaridæ there are animals with dextral organization occupying sinistral shells (*Lanistes*), while in the Planorbidæ the common Flat-coiled Water Snail (*Planorbis*) is an example of a normally sinistral animal in an apparently dextral shell. This is brought about by what is known as "hyperstrophy," and may be illustrated by taking a perfectly flat, coiled shell and placing it with the mouth downwards and directed away from the observer (Plate IV., Fig. 3, A); then in dextrally organized molluscs that assume a spiral growth, the spire would normally be exerted towards the right (Plate IV., Fig. 3, B, C), but may exceptionally be

exserted towards the left side (Plate IV., Fig. 3, *B', C'*). In the first case the shell will be dextral, in the latter sinistral. With sinistral animals these conditions are just reversed.

In certain forms (*Odostomia*, *Turbonilla*, *Tornatina*, etc.) the young shell is sinistral, after which dextral growth suddenly ensues, and the completed shell is dextral (Plate IV., Fig. 2). The term "heterostrophy" has been applied to this condition.

The axis, or "columella," of the shell is sometimes hollow, or "umbilicated" (the hollow itself being called the "umbilicus" (Plate VII., Fig. 9; and VI., Fig. 3); sometimes the whorls are closely coiled, and a solid pillar of shell results (Plate VI., Fig. 2). In the genus *Natica* the umbilicus is open, but in many of the species the cavity is more or less filled by a shelly deposit known as "callus" (Plate VI., Fig. 3, *A-E*). The "apex" or extreme top of the shell generally differs in markings and other features from the rest, and offers important characters. This "nucleus," or "protoconch," is the portion formed in the egg, hence it is also known as the "embryonic shell."

The spiral channel formed by the junction of the whorls is termed the "suture." A spiral line traced along the whorls midway between the sutures would mark the "periphery." The "mouth," or "aperture," has sometimes quite a circular margin (peristome), when it is said to be "entire" or "continuous";

more often it is "interrupted," the side next the columella being bounded by the wall of the body whorl only, when the exterior portion is known as the "outer lip" or "labrum," and the other side as the "inner," "columella lip," or "labium." There is frequently a notch in the margin of the aperture near the junction of the outer lip with the body whorl, and another where it joins the anterior end of the columella; these are respectively termed the "posterior" and "anterior canal," and give passage to the siphons of the animal. (All these terms are illustrated on Plate VI.) This group has been called "siphonostomatous," and those without any notch "holostomatous."

In some rhipidoglossate forms (*Pleurotomaria*, the fossil *Belerophon*, *Emarginula*, etc.) and the toxoglossate *Pleurotoma* there is a slit near the periphery of the labrum that gives passage to the anal fold or siphon. In others—*Haliotis*, etc.—the slit gives place to a series of perforations (Plate VII., Figs. 1-8. See also *infra*, pp. 94 and 95).

The labrum is thin and sharp in most shells, and in some adult forms; but more frequently it is either thickened, or curved outwards (reflected), or curled inwards (inflected), or expanded or fringed with spines. When these thickenings or expansions occur periodically during the growth of the shell, they form conspicuous transverse markings on the whorl termed "varices." The exterior of the shell

is also more frequently than not ornamented with either spiral lines or ridges running in the direction of growth, or with transverse markings coinciding with the lines of growth or with both (Plate V., Fig. 11-17).

The external spines that come in the way of the growth of the shell as whorl is added to whorl are dissolved in some way, and removed by the animal. In some cases also the internal walls of the whorls and the columella are similarly removed to make more room for the growing creature (*e.g.*, *Nerita*, *Theodoxis*, *Cypræa*, *Conus* [Plate VII., Figs. 12 and 13], *Auricula*, etc.).

On the other hand, when the animal in the course of growth leaves a space in the upper whorls, this is either filled up with a shelly deposit (Plate XXXII., Fig. 6), or cut off by the formation of a wall or septum across the whorl (Plate VI., Fig. 2, *s.m.*, and in *Vermetus*, etc.).* A similar partition is found when the apex of the spire becomes worn through or broken by accident, or attacked by boring Molluscs (Plate VII., Fig. 13), or is broken off as a regular successive phase of the animal's existence (*e.g.* in *Cæcum* [Plate VII., Fig. 14], *Rumina decollata* [Plate VII., Fig. 15], etc.).

Many of the Gastropods, like the Periwinkle, close the mouth of the shell, on retiring into it, with

* One, and only one, instance of this in a helicoid has been recorded—viz., in a species of *Glyptostoma*.

a trap-door (Plate VIII., Fig. 2), the "operculum"; when extended, this lies on the animal's back, and in many cases forms a sort of pillion on which the shell rests (Plate II., Fig. 1, and Plate VIII., Fig. 1). It consists of a horny layer, sometimes strengthened by the addition of shelly matter, which differs in structure from that of the shell itself. Its inner side is marked by the scar of the muscle which is attached to it, while outside it exhibits lines of growth. The operculum, various forms of which are shown on Plate VIII., Figs. 4-13, grows by additions made to the original point of beginning, the "nucleus," either all round, concentrically; or on one side, so that the nucleus remains at the end or at one side; or the growth may result in a spiral. This spiral is sinistral in dextral, dextral in sinistral shells. Nearly all the Gastropoda are furnished with an operculum in the young stage within the egg, and though some discard it on hatching out, the greater number retain it throughout life. Many of the spiral and concentric forms fit the mouth of the shell accurately, others only partly close the aperture, in yet others it becomes rudimentary, while in certain specialized forms, such as *Strombus* and its allies, it is converted into a sort of claw at the end of the elongated foot, and is used to assist the animal in progression (Plate VIII., Fig. 3).

A more peculiar means for blocking the entrance of the shell when the animal retires into it is possessed

by the genus of land shells called *Clausilia* (Plate VIII., Fig. 17). The "clausium" (*c*), as it is called, is a spoon or shoehorn shaped elastic plate, attached by its stalk to the columella within the shell, and closes automatically behind the retiring occupant.

One remarkable little Land Snail (*Thyrophorella*), inhabiting the island of St. Thomas, in the Gulf of Guinea, is said to be able to close the mouth of its shell by bending down a portion of the peristome which projects beyond the upper half of the aperture, and is furnished with a hinge for the purpose (Plate VIII., Figs. 18 and 19).

In many Gastropods, especially the Land Snails, the ingress of larger enemies is barred by projecting teeth placed round the aperture, or, less frequently, some way back in the shell. Sometimes these teeth are so long and numerous that it is a matter of wonder how the rightful owner itself gets in and out of its house (Plate VIII., Figs. 14-16).

The Gastropoda are divided into two sub-classes :

1. STREPTONEURA, in which the torsion of the visceral loop is well marked.

2. EUTHYNEURA, in which, in the adults, owing to partial detorsion of the visceral hump, the visceral loop nearly becomes once more simple.

Sub-Class 1: The STREPTONEURA (also known as PROSOBRANCHIA, because the gills are in advance of the heart), primarily by the gill structure and secondarily by the radula, are divided into—

Order I.: *ASPIDOBANCHIA*, having the gill filaments flattened out into leaf-like expansions.

Sub-Order 1: *DOCOGLOSSA* (Plate IX., Figs. 7-9; Radula, Plate III., Fig. 12), comprising the Limpet family.

Sub-Order 2: *RHIPIDOGLOSSA* (Plate IX., Figs. 10-24; Radula, Plate III., Fig. 13), comprising the Ormers (*Haliotidæ*), Keyhole Limpets (*Fissurellidæ*), etc., in which the older members still retain the right (originally left) gill, while the more specialized have only one, the left (originally right) gill.

Order II.: *PECTINIBRANCHIA*, having elongated gill filaments.

Sub-Order 1: *TÆNIOGLOSSA* (Plate X.), which includes the greater part of the sub-class, and in which the radula formula is generally 2 : 1 : 1 : 1 : 2 (Plate III., Fig. 15).

Sub-Order 2: *STENOGLOSSA*.

Tribe 1: *RHACHIGLOSSA* (Plate XI.), including the Whelks, Dog-Whelks, and their kind, and having a radula formula of 1 : 1 : 1 (Plate III., Fig. 17), although in higher members of the tribe this is reduced to 1 (Plate III., Fig. 18).

Tribe 2: *TOXOGLOSSA* (Plate XII., Figs. 1-5), of which the Cones and Auger Shells (*Terebra*) are the best-known examples. The radula formula is 1 : 0 : 1 (Plate III., Fig. 19), or exceptionally 1 : 1 : 1.

Sub-Class 2: The *EUTHYNEURA* fall into two orders and four sub-orders:

Order I.: OPISTHOBRANCHIA, so called because the heart is in front of the gills.

Sub-Order 1: TECTIBRANCHIA (Plate XII., Figs. 6-19), or those having shells, which are mostly fragile or rudimentary, and often concealed in the folds of the mantle. To this belong the Sea-Hares (Aplysiidæ), the Bullas, etc.

Sub-Order 2: NUDIBRANCHIA (Plate XII., Figs. 20-28), or the shell-less Sea-Slugs, are externally symmetrical animals, without true gills, respiration being effected by secondary gills, or by the general surface, aided in some cases by the "cerata," which are appendages of the dorsal integuments.

Order II.: PULMONATA, or the majority of land and freshwater shells, in which the true gill has disappeared, and its function is taken up by the wall of the mantle cavity.

Sub-Order 1: BASOMMATOPHORA (Plate XIII., Figs. 1-10), or those having eyes at the bases of the tentacles, embraces the freshwater pulmonates and a few land shells.

Sub-Order 2: STYLOMMATOPHORA (Plate XIII., Figs. 11-35, and Plate XIV.; Radula, Plate III., Figs. 21 and 22), or those having the eyes at the end of the "horns," takes in nearly all the land shells.

CLASS III.: The SCAPHOPODA, or SOLENOCONCHA (Plate XV., Figs. 1 and 2), of which the

Elephant's-Tusk Shell (*Dentalium*) is the type, form a single small group by themselves.

The animal is symmetrical, with a rudimentary head, and a long cylindrical foot used for burrowing in the mud in which these creatures live.

The borders of the mantle are united beneath, forming a tube, open at both ends, enclosing the rest of the body, and encased in the tubular shell, which is likewise open at both ends, there being no approximation of the two ends of the alimentary canal. There is generally a notch in the margin of the shell at the smaller end (or posterior opening) on the ventral or convex side. In one genus, *Schizodentalium*, there are, besides, in a line with and close to this notch, a series of openings. Sometimes the shell is finely striated lengthwise.

CLASS IV.: The PELECYPODA, or LAMELLIBRANCHIA (Plate XV., Figs. 3-9), commonly known as Bivalves, of which the Oyster, Mussel, etc., are familiar examples. In these the head is rudimentary, hence they were called ACEPHALA by Cuvier; while, because a head is present in the embryo but does not develop, Lankester proposed to term them LIPOCEPHALA. The characteristic radula is, of course, wanting in this group. The stone-axe-shaped foot is usually well developed, and serves as a burrowing and, rarely, as a creeping organ.

The symmetrically disposed organs of the body

are enclosed between the two, right and left, lobes of the mantle, which in their turn are covered by the two shelly plates, or valves. In a few instances the mantle is extended and reflected over the valves, and partly (*Galeommidae*) or completely (*Ephippodonta*, etc.) envelops them.

The mantle lobes are attached along the back and extend out to the margins of the valves. In the more primitive forms the mantle margins are quite simple, and open from the front round the ventral edge to the back; but many different modifications take place in the higher forms. Instead of the margins being simple, there may be folds, thickenings, protuberances, tentacles (Plate XV., Fig. 5), various glands, and even eyes (Plate XV., Fig. 8). Nor are the margins always free; indeed, in extreme cases they are united nearly the whole way round. There are various stages (Plate IV., Fig. 4, *A-F*): reckoning the open one as the first (*A*), then in the second (*B*), instead of the water being admitted all the way round, the edges of the mantle are kept closely applied to each other except where the foot protrudes and at two points at the hinder end, one of which serves to admit the fresh water to the gills, and is called the "inhalent aperture," whilst the other allows the fouled water to escape, and is termed the "exhalent aperture." In the next stage (*C*), the edges of the mantle are united permanently at the point between these two openings; and in the

fourth stage (*D*), at a second point below the inhalant aperture. In the fifth stage (*E*), the margins of these apertures have grown out into tubes ("siphons," Plate XV., Fig. 7), and the remaining portions of the mantle margins have united all round, except where the foot is protruded. Finally (*F*), the two siphons become united externally (Plate XV., Fig. 4). In these cases there is frequently a fourth small aperture left in the ventral margin. The siphons, the ends of which are often fringed, can be wholly or partly withdrawn.

The gills lie underneath the mantle, one on either side (Plate XV., Fig. 3, portion shaded with straight lines; and Fig. 8, *br*), in the space between the latter and the body of the animal. These organs vary progressively from a very simple structure to a very complicated one, and since their structure has been made the basis of the classification of the group, a brief description of it is necessary. In the more primitive Bivalves the gill is of the aspidobranch type (*ante*, p. 7, Plate IV., Fig. 5, *a*); but in the higher Pelecypods they are filibranch, only the filaments of each of the two rows, instead of remaining separate, have an arrangement whereby they interlock and form a continuous membrane, like the web of a feather. The mechanism by which this is brought about is extremely simple. At regular intervals on either side of each filament are little patches of stiff hairs which interlock with the corre-

sponding ones on the two neighbouring filaments, just as two brushes may be made to do; these are known as the "ciliated junctions" (Plate IV., Fig. 5, *E*). Moreover, the two membranes, "lamellæ," thus arising do not simply depend from the axis, but their edges are folded upwards so as to keep them within the margin of the shell. The outer lamella is folded outwards, and the inner inwards, so that they form a **W** in section (Plate IV., Fig. 5, *B*).

A further complication of structure ensues when junctions, called "interlamellar junctions," are formed between the dependent part of each filament and its reflected portion. In a more advanced stage still both the ciliated and interlamellar junctions become solid connections, so that the whole structure presents a sponge-like appearance, while the reflected ends of the filaments, uniting with the walls of the mantle and foot, subdivide the pallial chamber (Plate IV., Fig. 5, *C*). One further development there is, in which the gills have become converted into a sort of party-wall, separating the pallial chamber into a dorsal and ventral portion (Plate IV., Fig. 5, *D*).

At certain points all over the gill filaments there are powerful cilia, which by their action keep a brisk current of water flowing over the gills in a constant stream from behind forwards. This not only insures a fresh supply of oxygen, but conveys the micro-organisms on which the animal feeds towards the mouth.

The muscular foot is a prominent feature in most Bivalves, lying in the middle line towards the front of the body (Plate XV., Figs. 3, 6-8, *f*). Towards the back of it is situated the gland for spinning the horny threads by which many Bivalves anchor themselves to stones, etc. The Common Mussel and the Zebra Mussel are familiar examples, and the bunch of threads is known as the "byssus" (Plate XV., Fig. 9, *b*). The animal generally has the power of rejecting its byssus at any time and spinning a fresh one.

The mouth is situated a little behind and beneath the front adductor muscle; it is unarmed, neither jaw nor radula being present. It is flanked on either side by a pair of twin, triangular lobes, the "labial palps" (Plate XV., Fig. 3, *t*), which are in a line with, and in front of, the gills. Their function is apparently to collect, and possibly to taste, the food before it passes into the mouth.

Each valve of the shell is a hollow, irregular, shallow cone, the apex of which, termed the "beak," or "umbo," is the point at which growth began, and is, in fact, the young shell, or "prodissoconch": it generally differs in shape and markings from the later growth.

The umbo is usually curved more or less to one side (Plate XVI., Figs. 1 and 2, *u*), and generally points towards the head, or anterior end, when the shell is said to be "prosogyre," in contradistinction

to those in which the umbones are straight, "orthogyre," or are directed backwards, "opisthogyre." The last-named condition may be the pelecypod equivalent of hypertrophy in the Gastropod shell. More often than not the two valves are of equal size and shape, and the shell is "equivalve," as in the Cockle; sometimes, however, as in the Oyster, one valve is smaller than the other, and the shell is "inequivalve." The Bivalves are all more or less "inequilateral"—that is to say, if a line be drawn from the umbo to the ventral margin of the valve, the portion on one side of the line, usually the front one, will be found to be smaller than that on the other. When the shell is shut it is said to be "close" if the valves fit accurately, and to "gape" if openings be left (Plate XVII., Fig. 5).

Near the umbones the two valves are united by a chitinous "ligament" (Plate XVI., Fig. 2, *l*), formerly known under the misleading name of "cartilage," which is made up of an outer non-elastic layer and an inner, fibrous, elastic layer. The whole forms a sort of **C** spring which tends to open the valves, the act of closing being effected by two powerful "adductor" muscles that pass from one valve to the other, and are situated at either end of the axis of the body.

To prevent the opposed valves from shifting when closed, a series of projections, or "teeth," fitting into each other, are developed near the ligament.

They are sometimes numerous and all alike (Taxodont), especially in the more primitive Bivalves *Nucula*, *Arca*, etc. (Plate XVII., Figs. 1, 3, 6, etc.). More usually they are divisible into a central, more or less transverse, group of "cardinal teeth," flanked on either side by others running with the shell margin, or "lateral teeth" (Teleodont). This shell margin bearing the ligament and teeth is known as the "hinge line," and is sometimes extended inwards so as to form a sort of platform, the "hinge plate" (Plate XVI., Figs. 1 and 2). The number of teeth in the two valves differs, and occasionally, as in *Chama*, an individual will have the normal dentition of the two valves reversed, a condition apparently corresponding as near as such may be to sinistrosity in the Gastropod. The teeth become exceptionally strong in shells that live in situations exposing them to strain, and dwindle and disappear in such as dwell in protected localities.

The possibility of the valves being laterally displaced is further guarded against in very many by tooth-like crenulations of the ventral margins of the valves that interlock, as in the Scallops, Cockles, etc. (Plate XV., Fig. 8; Plate XVIII., Fig. 3).

The shelly tubes secreted by the Ship-worm (*Teredo*, Plate XX., Fig. 5), *Gastrochaena* (Plate XIX., Fig. 16), the Waterpot Shell (*Brechites*, Plate XX., Fig. 19), and some others to line their burrows are produced, it is true, by extensions of the mantle or

cuticular surface of the animal, but are distinct from the real shells, which in the *Teredo* and *Gastrochaena* are within the tube and free, while in *Brechites* they are built into its wall.

The points of attachment of the adductor muscles to the shell are marked by well-defined scars (Plate XVI., Figs. 1-3, *a.a.* and *p.a.*). Close to the posterior adductor scar, that of the muscle for withdrawing the foot (Plate XVI., Figs. 1-3, *p.v.*) is found, and minor scars occur nearer the umbones of the valves to which other small muscles are attached. Running from one adductor scar to the other, at a short distance from the ventral margin of the shell, is a shallow groove, the "pallial line" (Plate XVI., Figs. 1-3, *p.l.*), which marks the attachment of the mantle edge. In those molluscs that have large retractile siphons, room has to be made for these, and the pallial line, instead of forming a continuous curve, takes, shortly before it reaches the posterior scar, a sharp bend backwards towards the centre of the valve, forming a bay or sinus, known as the "pallial sinus" (Plate XVI., Fig. 2). The size of this sinus naturally corresponds to that of the siphons.

In some Bivalves, such as the Common Mussel of the seashore, the posterior portion of the body is more developed than the anterior. This development tends to bring the two adductor muscles and the hinge into a line, and in proportion to render

the anterior adductor superfluous, with the result that it tends proportionately to dwindle and disappear, leaving the enlarged posterior muscle to do the work of both, as in the Oyster and Scallop (Plate XVI., Fig. 3, *A-D*). Bivalves with two adductor muscles are termed "Dimyaria"; and if the latter are of equal size, are said to be "Isomyarian"; or, if unequal, "Heteromyarian"; whilst those having only one are called "Monomyaria."

The Pelecypoda are subdivided, according to the structure of the gills, into four orders:

Order I.: PROTOBRANCHIA (Plate XVII., Figs. 1-3), in which the gill-filaments take the form of flattened, leaf-like expansions (Aspidobranch, Plate IV., Fig. 5, *A*). To this order the Nut Shells (*Nucula*) and their allies belong, and probably also the earliest known Bivalves, forms now quite extinct, that have been termed "Palæoconcha." With few exceptions they have a taxodont hinge.

Order II.: FILIBRANCHIA (Plate XVII., Figs. 5-17), having long, parallel gill-filaments, the ends of which are folded up, forming a **W** in section, and locked together by ciliated and sometimes interlamellar junctions (Plate IV., Fig. 5, *B*). To this order the Ark Shells, Mussels, and Pectens belong.

Order III.: EULAMELLIBRANCHIA (Plates XVIII., XIX., and XX., Figs. 1-19), in which the elongated filaments are yet longer, more folded up, and permanently united at intervals till they form a com-

plete spongy network (Plate IV., Fig. 5, C). The Oysters, freshwater Mussels, Cockles, Venus Shells, Myas, and Ship-worms are examples of this order.

Order IV.: SEPTIBRANCHIA (Plate XX., Figs. 20-23), in which the gill-filaments are completely fused and transformed into a continuous muscular septum, with several perforations to admit of the circulation of the water (Plate IV., Fig. 5, D). A few deep-water forms (Poromyiidæ, Cetoconchidæ, and Cuspidariidæ) constitute this order.

CLASS V.: The CEPHALOPODA (Plate XXI.), of which the Nautilus, the Cuttlefishes, and Octopods are examples, includes some of the most highly organized of the Mollusca, as well as the largest, for certain of the Cuttlefishes, it is calculated, exceed 50 feet in length.

The Cephalopoda are symmetrical animals, the two halves of the body corresponding in structure.

The head, on either side of which there is a large and well-developed eye, is more or less distinct, and is surrounded by the foot, which has, so to speak, grown round it (Plate XXI., Fig. 1). In the Nautilus the margins of the foot are divided into lobes, each bearing a group of tentacles furnished with suckorial ridges, that are retractile within special sheaths (Plate XXI., Fig. 2). In the other groups the pedal appendages take the form of four or five pairs of elongate "arms," these arms being furnished with rows of suckers or of hooks.

The mouth lies in the centre of these arms, and is furnished with a pair of powerful chitinous jaws that resemble a parrot's beak (Plate III., Fig. 4); while the radula, though proportionately small, is well developed (Plate III., Fig. 20).

The symmetrical body is surrounded by the bell-shaped mantle, covered in some cases by a shell, while those without an external shell frequently have lateral fins.

On the ventral side a cavity is left between the mantle and the body (Plate XXI., Fig. 3, *m.c.*). In this "mantle cavity" the gills (*g*) are placed, and into it the termination of the reflexed alimentary canal opens, as well as the ink-sac (*i*), with which most members of the class are provided.

Just at the mouth of the mantle cavity two lobes of the skin above the foot, sometimes free and sometimes united at their margins, form a "funnel" or "siphon" (*f*). Through this siphon the water is discharged from the mantle cavity; quietly during ordinary respiration, or with great force when the creature propels itself backwards through the sea by means of the ejected stream. Through the same orifice the animal can at will eject the inky fluid from the ink-sac, with which it clouds the water on emergency when seeking to escape its foes. This power is possessed by all the living Cephalopoda save *Nautilus*, *Cirroteuthis*, and two species of *Polypus*. An ink-sac was present in the fossil Belemnites, and

there is a picture in the possession of the Geological Society of London representing the fossil head of a reptile (*Ichthyosaurus*) executed with the fossil sepia from a Belemnite preserved in the same strata.

The gills of the Cephalopoda are aspidobranch in type, and either four or two in number: the class is consequently divided into Tetrabranchia and Dibranchia.

Among the Cephalopoda we meet, for the first time in the Mollusca, with internal structures of great import—namely, cartilages—which are especially developed in the head. In *Nautilus* there is an H-shaped cartilage, which supports the ventral portion of the nerve centres, two of its branches extending to the base of the funnel. In the Dibranchia a cartilage completely invests the central nervous system, the œsophagus passing through it. Different Cephalopoda have additional cartilaginous pieces in other parts of the body, such as the bases of the fins and arms, at the base of the neck (when the mantle is not fused to the head), at the internal extremities of the retractor muscles of the head and funnel, and even in the two branchial lamellæ.

The shell, as seen in its fullest (external) development in the *Nautilus* and its fossil relations, as well as in the Ammonites, resembles that of the Gastropoda in consisting of a single conical tube. In the earliest kinds of *Nautilus* (*Orthoceras*) the shell is quite straight, in some others it is curved; but in

the majority of Nautiloids and Ammonites it is more or less coiled discoidally, and generally the coil is in a forward direction over the animal's back, or "exogastric." A few, however, are coiled in the reverse direction, or are "endogastric"; while in some cases the coil is produced into a helicoid, or even a turriculated spire. In yet other instances the shell may be coiled in the young state, and become more or less uncoiled (*Scaphites*, *Crioceras*, *Hamites*, etc.) or even straight (*Baculites*) in the adult (Plate XXII.).

The striking feature of the Cephalopod shell, however, lies in its internal structure (Plate I.). As the animal grows, it builds on to the open end of the shell to obtain increased accommodation, just as the Gastropod does; but since it grows in girth more than in length, it has, in order to obtain the requisite space, to shift bodily forward in its shell. This takes place gradually by the forward growth of the shell muscles on either side and the intervening pallial attachments ("annulus") till an unoccupied space is thus left behind, which is then partitioned off by a shelly wall ("septum"); in this way the series of chambers, so familiar in sections of the Nautilus shell, are formed, each marking the completion of a period of growth. The septa are, however, not entire, a perforation in each is connected with that in its neighbour by a pipe, in part calcareous, in part chitinous, the whole forming a continuous tube which passes from the outermost chamber, or that occupied by the animal,

through all the preceding ones to the apex of the shell. This tube, or "shell siphuncle," covers a prolongation of the mantle, the function of which is not quite clear. The margins of the perforation in each septum are produced on one side into a short neck: these necks in the Nautiloidea and the most primitive of the Ammonoidea all point backwards; in the other Ammonoidea they point forwards. Further, the margins of the septa, where they join the outer shell, form a simple curve in the Nautiloidea, whereas the "suture-line" in the Ammonoidea becomes highly folded (Plate XXI., Fig. 5). Another feature of interest distinguishes the shells of these two sub-orders; in the Nautiloidea the protoconch is not calcareous, and the only trace left of its existence is a scar on the exterior termination of the first chamber; in the Ammonoidea the protoconch is calcareous and preserved.

The chambers of the shell of *Nautilus* (and presumably the same was true of the Ammonites) during the life of the animal are filled with air containing more nitrogen than is found in atmospheric air. This gives great buoyancy to the shell, and so permits of the animal swimming rapidly.

In *Spirula* alone of living Dibranchia the shell is partly internal (Plate XXV., Fig. 1), and the same was probably the case with some fossil forms; but in all other members of the order the shell is completely internal, and frequently rudimentary, while in the

Octopods there is no longer any true shell, but only some simple chitinous rudiments, to which the retractor muscles of the head and funnel are attached. In certain fossil Dibranchia (*Belemnites*, etc., Plate XXIII.) the internal chambered shell, known as the "phragmocone," is enclosed in a pointed calcareous sheath, or "guard," at the end opposite to the head, while from the dorsal margin of the anterior end of the phragmocone there arises a broad, thin, chitinous plate, called the "prostracum." To modifications in form of these three constituent parts, or to the partial or total suppression of one or more of them, the resultant differences between the internal shells of the other members of the order may be traced. This, however, will be better gathered from the diagrammatic figures on Plate XXIV. than from any lengthy description.

The shell of the Paper Nautilus, or Argonaut (Plate XXI., Fig. 4; Plate XXV., Fig. 12), stands on a different footing to the ordinary shell, and does not originate in the shell-gland; it is only formed some days after the creature is hatched, and is peculiar to the female, being chiefly used as a vehicle for carrying and protecting the eggs, which, when deposited, are agglutinated to it. It is exogastric, and composed of three layers, of which the outer and inner are alike and prismatic, while the middle one is fibrous: there is no pearly layer within. The animal is not attached to it in any

way, and the shell is principally held in place and protected on the exterior by the anterior pair of arms, which are furnished with web-like expansions for the purpose. The ends of the remaining arms, which are carried folded back over the animal's body, are tucked into the shell, and seemingly also assist in retaining it by the aid of the suckers. It is commonly stated that the shell is entirely the product of the pair of webbed arms, and that once the animal quits its tenement it cannot re-occupy it; but both statements are incorrect. The latter has been shown by actual observation to be the reverse of fact, while the occurrence of fractured shells, showing evidences of repair from the inner side, upsets the former statement, which is otherwise wanting in probability. The more reasonable supposition is that the shell is mainly secreted by the mantle covering the visceral dome, and that the webbed arms, which are also furnished with secretory cells, contribute to the exterior and assist in moulding it, during formation, to the animal's body.

The Cephalopoda are divided into—

Order I.: TETRABRANCHIA (Plate XXII.), or those having four gills and an external shell. The funnel is in two parts, and the eyes are open, having no crystalline lens.

Sub-Order 1: NAUTILOIDEA, or the Nautilus and its allies.

Sub-Order 2: AMMONOIDEA, or the extinct group

of Ammonites and their kindred, that from the close parallelism of their shells, by which alone they are known, were probably similar in structure to the Nautiloidea, and are therefore better classed with them than in a group apart.

Order II.: DIBRANCHIA (Plate XXV.), or those having only two gills, and the shell generally more or less internal. The funnel is a complete tube, and the eyes have a crystalline lens.

Sub-Order 1: DECAPODA, or those with ten arms. Two of these, the "tentacular arms," situated on each side between the third and the last pair, are more or less retractile into special pouches, and as a rule only bear suckers at their free extremities. The eight ordinary arms are shorter than the body. There is generally a fairly well-developed internal shell, and usually lateral fins.

Two tribes are distinguishable: (a) Those (Oigopsida) in which the cornea covering the eye is incomplete—*i.e.*, has an aperture left. This includes *Spirula*, many of the Pen-and-Ink Fishes, and probably such fossil forms as the Belemnites, *Belemnoteuthis*, etc. (b) Those (Myopsida) in which the cornea is complete, like the Common Cuttle (*Sepia*), the Common Pen-and-Ink Fish (*Loligo*), and their fossil kindred.

Sub-Order 2: OCTOPODA, or those with eight similar arms all longer than the body.

These again fall into two tribes: (a) LEOGLOSSA,

in which the radula is wanting and the arms are united by a membrane, while fins are developed on the body. Some pelagic (*Cirrotenuthis*) and deep-sea forms (*Opisthotenuthis*) belong here, and possibly also the fossil *Palæoctopus*. (b) TRACHYGLOSSA, the members of which have a radula, but no true fins. The Common Octopus (*Polypus vulgaris*) and the Argonaut are familiar examples of this tribe.

Of the interrelationships of these five classes it is impossible to say much in the present state of our knowledge, beyond that the first four are the more closely related.

CHAPTER III

GEOLOGICAL HISTORY

THE Mollusca made their appearance very early in the world's history, and, as might be expected, on the whole the more generalized forms preceded the more specialized. It has, of course, to be borne in mind that many of the conclusions here epitomized have been drawn of necessity from shell characters alone, and are consequently liable to modification with possible advance of knowledge.

In the oldest fossiliferous beds, belonging to the Lower Cambrian epoch, only a few representatives have been found. These consist of some Limpet-like shells that have been referred in part (*Scenella*) to the Docoglossa, and in part (*Stenotheca*, *Platyceras*) to the Tænioglossa. These last, however, it has been suggested are, instead, descendants of the primitive Mollusca (*Prostreptoneura*) that gave rise to the Gastropod branch. With these is a turreted, convolute shell (*Rhaphistoma*) representing the older, or two-gilled, section of the Rhipidoglossa, and the

remains of two Bivalves. One of these Bivalves (*Modioloides priscus*) is known only by the internal cast, 2 millimetres long, and appears to belong to the Protobranchia, or oldest order, while the other (*Fordilla*) may prove to be a Bivalve crustacean and not a mollusc at all.

In the Upper Cambrian further examples (*Murchisonia*, *Cyrtolites*, *Owenella* and *Straparollina*) of the early Rhipidoglossa are found, as well as one (*Trochonema*) supposed to belong to the higher one-gilled section of that sub-order. Another Gastropod (*Subulites*) of doubtful affinities, but almost certainly belonging to the Pectinibranchs, and having a siphonostomatous shell, shows that three out of the four principal divisions of the Streptoneura were already represented at this early stage. Already, too, seven species of Cephalopoda had made their appearance. They all belong to the more primitive Nautiloidea, and, with one exception, the straight-shelled section of that group.

During the succeeding Ordovician epoch the Aspidobranch Gastropods predominated, their ranks reinforced by representatives (*Cyclonema*) of the Top-Shells (Turbinidæ) that belong to the more specialized one-gilled section, while *Holopæa* and *Scalites* were added to the Tænioglossates. Pelecypods were still rare, the Protobranchs were represented by *Ctenodonta*, and the more specialized Filibranchs by *Cyrtodonta* and *Eopteria*. The epoch also produced the

first known Chiton (*Priscochiton*). The Cephalopoda had increased in number to sixty-five species of Nautiloidea, the majority still being straight-shelled, but some curved and a few coiled forms (the first) are included.

With the Silurian epoch a considerable increase in the number of Mollusca becomes evident. To the Gastropods are added members of the families Trochidæ, Epitoniidæ, and Xenophoridæ. Among Pelecypods, Palæoconchs were most abundant, but all orders save the Septibranchs were represented. Two more Chitons (*Helminthochiton* and *Chelodes*) made their appearance, and shells that have been referred, though doubtfully, to Scaphopoda. The most marked feature of the epoch, however, was the abundance of the Nautiloidea, which then attained their zenith with about 230 species, among which coiled were almost as abundant as the other shell forms. From that day the group has steadily diminished in numbers, only five species now existing, or as some reckon them, fewer still.

The Devonian strata have yielded evidence of the further increase in the Pelecypods, representatives of the Filibranch families—Trigoniidæ, Pectinidæ, and Mytilidæ—appearing with the Eulamellibranch families—Pinnidæ, Cardiniidæ, Megalodontidæ—and such specialized forms as *Pholadella* and *Allorisma*, the latter being the earliest example of a Pelecypod, showing clear evidence of retractile siphons. Of

most note, however, is the advent on the scene of the first freshwater Mussel, *Archanodon Jukesii*, which is closely allied to, and greatly resembles, the modern *Anodonta* (Swan Mussel) of our ponds and lakes. A true Scaphopod (*Dentalium*) and representatives of the more primitive Ammonoidea (*Clymenia*) and the Goniatites likewise came into existence in the Devonian epoch.

Just at the close of the Devonian epoch the first evidences are met with of the existence of Land Snails (*Strophites*, *Dendropupa*, etc.) allied to the Chrysalis Shells (Pupillidæ); these were found in the plant beds at St. John, New Brunswick. The Coal-Measures of the succeeding carboniferous period have yielded some other interesting air-breathing Snails, including the oldest known terrestrial Rhipidoglossate (*Dawsonella*); the first brackish-water Snail (*Ampullaria*); the earliest freshwater Snail, (*Physa*), both these last belonging to genera well known at the present day, besides the oldest known species (*Zptychius*) of the most primitive of Pulmonates, the Auriculidæ, as well as other species of *Dendropupa* and a small Land Shell,* closely allied to the genus *Pyramidula*, which is a common form to-day. Further examples of freshwater Bivalves belonging to the family Cardiniidæ were plentiful in the Carboniferous, from which, too, the oldest example of a Tectibranch (*Cylindrobullina*) has been

* Still miscalled *Zonites* in textbooks.

obtained, and the first evidence of the highly specialized Bivalve (*Lithophagus*) that burrows into rock, shell, or coral.

At the close of the Palæozoic period many of the older genera of Bivalves disappeared, but at the opening of the Mesozoic period in the Trias, a number of others came in. Among them further representatives of the freshwater Mussels (*Unio*), of the Thorny Oyster family (Spondylidæ), and the Cockles (Cardiidæ). The oldest examples (*Campylosepia*, *Aulacoceras*, and *Atractites*) of the group of ten-armed Cuttlefish made their appearance also at this time.

The Jurassic strata are rich in Molluscan remains, which sometimes form whole masses of rock. The Rhipidoglossate Gastropods attained their acme of development at that period, while Pectinibranchs multiplied in great variety, and representatives of the higher forms began to appear. Further remains of Land Shells (*Helix*, etc.) and the earliest examples of freshwater Gastropods (*Planorbis*, *Valvata*, and *Melania*) have been recorded from the lowest Jurassic beds, but there is some doubt as to the exact determination of these genera in most cases. In the uppermost beds, however, the well-known Purbeck marble is composed of masses of *Valvata*, *Vivipara*, etc.

Among Bivalves genuine Ark Shells (*Arca*), *Anomia*, and various families of Eulamellibranchs,

including the freshwater Cyrenidæ, made their appearance; while if *Corburella* be admitted as a member of the Septibranchia, that order must be added for the first time. The "pens" and ink-sacs of earlier members of the *Sepia* tribe (*Beloteuthis* and *Geoteuthis*) are first found in the Lias, with the remarkable Belemnites whose "guards," often called "thunder-bolts," are familiar fossils.

In the succeeding Cretaceous period further development took place. Among the Gastropods there was a decided increase in the higher Pectinibranchs, including representatives of most of the families of Rhachiglossa. Amongst Bivalves two most remarkable aberrant families (Radiolitidæ and Hippuritidæ) were confined exclusively to this period. Externally these look not unlike simple corals with a lid, while internally they display highly peculiar modifications. Numerous other Eulamellibranchs, including some boring forms such as Petricolidæ and Saxicavidæ, as well as the Razor-fish (*Ensis*), arose, with an undoubted representative of the Septibranchs (*Leiopistha*). An Octopus (*Palæoctopus Newboldi*) standing for the highest Cephalopods was revealed for the first time in the Cretaceous of Mount Lebanon, but, on the other hand, the Ammonites and Belemnites died out.

During the Tertiary epoch the Rhachiglossa and Toxoglossa became the dominant Gastropods, while the Bivalves showed an approximation to present

conditions. A great majority of the Lower Tertiary (Eocene and Oligocene) genera still exist, but none of the species. During the succeeding Miocene a few species, which are still in existence, made their appearance, while of the Pliocene species 80 or 90 per cent. are represented in the recent fauna.

At the close of the Eocene the wide distribution of many types now characteristic of warm, temperate, or tropical waters, began to be restricted, and during the Miocene the faunal boundaries of the Mollusca were mapped out nearly on existing lines. This was more true of the non-marine forms; but not till the Pliocene did each geographical province come to assume its present distinctive features.

CHAPTER IV

PRESENT HISTORY AND DISTRIBUTION

WITH such a past history as just recorded, it is little wonder that the Mollusca both have been and are abundant.

In 1866 a rough estimate gave the number of extinct species as 18,568, and living ones as 20,502. The list has been considerably extended since that time, and though no further estimate of the fossil forms appears to have been attempted, a recent calculation puts the number of living species known at the end of last century at upwards of 50,000. This total may be distributed among the five classes as follows: Amphineura, 600; Gastropoda, 40,100; Scaphopoda, 230; Pelecypoda, 8,600; Cephalopoda, 470.

Naturally, too, so ancient and so numerous a race is widely distributed over the surface of the globe to-day, and its members have become adapted to very varied conditions of life. The majority are marine, and mostly confined to the littoral and

laminarian zones (*i.e.*, between tide-marks; and so far as the seaweeds grow, or to about fifteen fathoms); a smaller number inhabit the deeper nullipore or coralline zone; whilst a few stragglers are met with at great depths. In all cases the nature of the sea bottom governs their individual distribution. Certain forms frequent the rocks, others sandy or muddy sea-floors. Some, on the other hand, spend their lives in the surface waters of the open sea.

The brackish waters of estuaries and lagoons are tenanted by a few kinds, including the strange pulmonate *Amphibola* (Plate XXVI., Fig. 23); while rivers, streams, and lakes are the dwelling-places of a considerable number. On the land, every spot capable of supporting life yields its quota of Mollusca, and the total number of known terrestrial species is consequently very great, and yearly being added to.

As will presently be mentioned, some forms will normally trespass out of their regular habitat, but certain more exceptional cases of interchange between marine and freshwater haunts may be appropriately alluded to here. Freshwater Snails sometimes become accustomed to salt-water conditions; thus, at Bornholm, in the Baltic, specimens of *Limnaea* and *Theodoxis* have been found living in company with marine molluscs in water containing as much as 1 to 1·5 per cent. of salt. In Southern Algeria *Melania* and *Melanopsis* inhabit waters surcharged with salt, where the marine Cockles failed to survive.

Experiments conducted many years ago show that species of the pulmonate genera—*Limnæa*, *Physa*, *Planorbis*, and *Ancylus*—can be habituated by the gradual addition of salt to as much as 4 per cent. in the water; so, too, but less easily, can the Prosobranchs *Vivipara*, *Bithynia*, and *Theodoxis*; while the Pelecypods *Anodonta*, *Unio*, and *Sphærium* die before that degree of salinity can be attained. Conversely, marine forms can be gradually accustomed to fresh-water existence: the Mussel (*Mytilus*) very easily; the Cockle (*Cardium edule*), the Oyster, the Common Limpet (*Patella vulgata*), *Turbo neritoides*, and others, less successfully. In these experimental cases, however, propagation would not take place.

On the rocks by the margin of the sea, within reach only of the splash of the waves, or of the water at the highest tides, will be found certain of the Periwinkles (Littorinidæ)—a situation in which they are joined by such of the Pulmonates as several of the Auriculidæ and the slug-like *Oncidium*, that dwell close down by the sea margin.

A little lower down, just below high-water mark, those strange Limpet-like Pulmonates, *Siphonaria*, *Gadinia* (Plate XXVI., Figs. 24 and 25), and the recently discovered *Aporemodon*, that have partially reverted to marine life, are to be found.

Between tide-marks the Chitons, Limpets (Patellidæ), Keyhole Limpets (Fisurellidæ), Ormers (Halio-tidæ), and similar molluscs, cling to the rocks or the

under surfaces of big stones. The Mussels, as well known, attach themselves to the rocks by their stout byssus threads, their clustered masses affording secure shelter to many lesser animals; while in mangrove swamps the Oysters will attach themselves to the branches of the trees that dip in the water at high tide—a fact which was observed and recorded by W. Smith at Sierra Leone in 1726.

Periwinkles, Top Shells (Trochidæ and Turbinidæ), and other holostomes, haunt the tangled masses of seaweeds; while among the siphonostomes are the Dog-Periwinkles (*Purpura*), Dog-Whelks (*Nassa*), etc., all stout-shelled forms capable of withstanding considerable buffeting amid the waves. The Piddock, or *Pholas*, *Saxicava*, *Lithodomus*, and other boring molluscs, excavate burrows in various rocks, in coral, and even the shells of their bigger confrères. Others, like *Tapes* and *Coralliophaga*, too lazy to make their own retreats, take possession of the deserted burrows of others. The latter generally selects the crypt of a dead *Lithodomus*, which it closely resembles in shape (Plate XXXII., Figs. 17 and 18), and the shells of successive generations of *Coralliophaga*, packed one within the other, will be found lying between the valves of the original architect of the home. In the cracks and crevices of the rocks the Octopods hide. The majority of the Pelecypods, such as the Cockles, Ark-Shells, *Tapes*, etc., remain more or less buried in the sand or silt, the Razor-fish

(*Ensis*) sinking itself well below the surface. Some species of *Lima* and *Volsella*, on the other hand, construct a sort of nest out of all kinds of marine refuse, held together by the threads of the byssus. The *Dentalium*, again, buries in the sand, leaving only the apex of the shell protruding.

The quieter waters of the laminarian zones are also tenanted by many of the foregoing, but they are especially the haunt of the Sea-Slugs (Nudibranchia, Plate XII., Figs. 20-28), as well as certain Opisthobranchs, like the Sea-Hare (*Aplysia*), and the smaller Gastropods, with the Oyster and other Bivalves.

The yet deeper regions of the coralline and nullipore zones are the special resort of the large Whelks (*Buccinum undatum*, *Neptunea antiqua*, etc.), Naticas, and other carnivorous Gastropods, of the Scallops (*Pecten maximus*, *P. opercularis*, etc.), *Pinna*, many of the Venus Shells, and other Bivalves. Here, too, the strange Aplacophora frequent the oozy areas.

Down to a depth of 300 fathoms there is a considerable number of deep-sea representatives of the Mollusca, mostly of the smaller and more delicate kinds, while a few abyssal examples are found at very great depths.

So far the extreme depths for each class that have been obtained were all recorded on the Challenger Expedition. Thus, a Chiton (*Leptochiton benthus*) was dredged at a depth of 2,300 fathoms in the Pacific Ocean; of Aplacophora, two immature

examples of *Chætoderma* off Nova Scotia at 1,250 fathoms. A Gastropod (*Stylifer brychius*) was brought up in the South Atlantic from a depth of 2,650 fathoms; a Nudibranch (*Bathydoris abyssorum*) in the Pacific Ocean from 2,425 fathoms; and some Pelécypods also in the Pacific from 2,900 fathoms; while a Scaphopod (*Dentalium leptoskeles*) was obtained from 2,600 fathoms off the south coast of Australia. Cuttlefishes have been taken from between 2,000 and 3,000 fathoms, but some uncertainty attaches to the records in their case, since none of the forms obtained at these depths were distinctly dwellers on the sea-floor.

No hard and fast line can be drawn between the several zones above enumerated, and some species range over more than one of them; nevertheless, the prevailing forms in each serve to distinguish them.

Conspicuous and most abundant among the ocean-swimming molluscs are the Sea-Butterflies (Plate XXVI., Figs. 1-16), formerly grouped in a class, as Pteropoda, but now recognized as highly specialized Tectibranchs—those with shells branching off from the Bulla-like section, while the shell-less ones are more nearly related to the Sea-Hares (Aplysiidæ). Less abundant are the Heteropoda (Plate XXVII., Figs. 17-22), now known to be free-swimming Tænioglossa, although they, too, were once classed apart. A Nudibranch (*Phyllirrhoë*) similarly specialized, and the Tænioglossate (*Ianthina*), with countless fry

of many species, also pass their lives far from land, with the larger number of the Cuttlefishes.

A more peculiar pelagic assemblage is afforded by those molluscs that dwell among the Gulfweed (*Saragassum*). They comprise a series of Nudibranchs, some of which are peculiar to the locality, a Tænioglossate (*Litiopa*), and two or three Limpets (*Helcion* and *Lepeta*).

Just as some representatives of the race have crept down into the depths, so others have ascended the rivers, and there become accustomed to a freshwater existence.

In the brackish water near the mouths of rivers, and occasionally for long distances up the rivers themselves, some stragglers from the marine host are to be met with, such as *Cerithium*, *Littorina*, *Nerita*, *Mytilus*, *Cardium*, *Macoma*, *Mya*, etc., where they may be found dwelling side by side with freshwater kinds. The genus *Theodoxis*, of course, has both marine and freshwater species, while there are freshwater representatives of the Ark-Shells, such as *Scaphula pinna*, of *Volsella*, and of the Piddocks, *Pholas rivicola*, and others.

There is, however, a distinct brackish-water group, including Gastropods belonging to the Tænioglossate genera *Potamides*. Certain of the Paludestrinidæ, *Assemania*, *Truncatella*, the Pulmonate *Chilinia*, and Pelecypods such as *Iphigenia* and *Scrobicularia*.

The true freshwater forms consist solely of Gastro-

poda and Pelecypoda. The former include some species of the Rhipidoglossate *Theodoxis* and its relative *Septaria*; Tænioglossate families such as the Viviparidæ, Ampullariidæ (a completely amphibious clan), Valvatidæ, most of the Paludestrinidæ, Melaniidæ, Typhobiidæ (in Lake Tanganyika), and Pleuroceridæ; Rhachiglossate forms as *Canidia*, *Clea*, and *Nassodonta*, and Pulmonate families as Limnæidæ, Planorbidæ, Ancyliidæ, Physidæ, commonly known as Pond Snails (Plate XIII., Figs. 1-7). The Pelecypoda belong mostly to the Sub-Mytilacea, and include the big family Unionidæ, or freshwater Mussels, of which the United States boasts no less than about 530 species, or more than half of those known; with their kindred the Mutelidæ; the freshwater Oysters, Ætheriidæ, of the African and American rivers; the Rangiidæ, Cyrenidæ, and the interesting Zebra Mussel (*Dreissensia*, Plate XV., Fig. 9). A freshwater representative of the Veneracea (*Glaucomya*), occurs in South-East Africa.

All these, like their marine confrères, more or less sort themselves according to their surroundings.

The Limpet-like *Ancylus* (Plate XIII., Fig. 1) and *Septaria* cling to rocks in swift streams. Other Gastropoda hide in the water-weeds, or crawl on the muddy banks. The Bivalves mostly dwell in the mud, but *Dreissensia* attaches itself by its byssus to rocks, etc., in moving water; and many of the small Cyrenidæ (*Sphærium*, Plate XVIII., Fig. 16,

and *Pisidium*, Plate XV., Fig. 6) climb about in the weed. Freshwater Mollusca are also not infrequently found living in water-pipes and cisterns connected with artificial supply.

Altitude has no terrors for the freshwater Mollusca, *Limnæa Hookeri* having been taken at a height of 18,000 feet above the sea. On the other hand, at a depth of 180 fathoms in Lake Baikal, some Paludestrinidæ peculiar to those waters have been met with. The most northern occurrence of a freshwater Snail is that of *Aplecta hypnorum* (a British species) which in Siberia attains as far north as 73° 30' in the Taimyr Peninsula.

Just as the marine Mollusca break their bounds, so will the freshwater pass theirs, and essay to trespass on the land. The Limnæidæ commonly crawl on the wet banks out of the water and in moist spots where swamp-loving terrestrial Pulmonates, like the Amber-Snails (*Succinea*, Plate XIII., Fig. 14), etc., love to pass their existence.

Among marine forms found on land may be named a remarkable Periwinkle, *Cremnoconchus*, which occurs only on wet cliffs in the Ghâts of Southern India, thirty to fifty miles from the sea. Another Periwinkle, *Littorina arboricola*, lives on trees fully 100 yards from the backwaters of Trincomalee Harbour, and is never known to enter or be covered by the water. The Rhipodoglossate, *Neritodryas*, a relative of *Theodoxis*, occurs on trees of some height in the

Philippines at a distance of a quarter of a mile from any water. The freshwater *Ampullaria* has been said to have been met with also on a tree-top. *Geomelania*, a genus closely related to the brackish-water *Truncatella*, is completely terrestrial.

The true terrestrial Mollusca comprise representatives of the Rhipidoglossa in the families Despoenidæ, Helicinidæ, and Hydrocenidæ; of the Tænioglossa in the Aciculidæ, Pomatiidæ [= Cyclostomatidæ], and Cyclophoridæ; and of the order Pulmonata, certain of the Auriculidæ among the Basommatophora, with all the Stylommatophora.

They flourish on every portion of the habitable land surface from the margins of the seas to lofty elevations on mountain peaks, a Slug, *Anadenus*, reaching the altitude of 16,400 feet in the Himalayas; while the record for farthest north for a Land Snail would appear to be held by *Vitrina angelica*, which is said to extend as far as latitude 72° in Greenland.

Some, like *Cæcilioides*, the Corsican *Helix tristis*, and *Testacella* (Plate XIV.), live underground—the first named entirely so. Most prefer damp situations at the roots of plants and shrubs, under fallen wood, beneath stones, or in the crevices of rocks; many are fond at times of ascending plants and shrubs, and do so more often than is commonly thought; other kinds are entirely arboreal. A few that inhabit arid and hot countries can withstand the full glare of the sun as they rest on rocks exposed to its rays. In the Egyptian desert Dr. Andrews says that each

scattered bush has its complement of *Helix desertorum* (Plate XIII., Fig. 34), while the ground beneath is strewn with the dead shells of past generations.

All the terrestrial Snails are chiefly crepuscular or nocturnal in their habits, but will issue forth on cloudy or wet days.

While the haunts of the Mollusca are similar in all parts of the globe, the distribution of the various members over the world's surface differs, just as it does in other divisions of the animal kingdom, on account of the differences of environment.

Obviously the geographical distribution of the Mollusca falls primarily into "marine" and "non-marine."

Dealing with the marine first, it is found that the pelagic forms are the more widely distributed, but may nevertheless be described as belonging to polar and tropical provinces. The North and South Polar forms differ: *Clione limacina* and *Limacina helicina* belong to the former; while among the latter are *Limacina antarctica* and *Spongiobranchia australis*. *Argonauta*, *Hyalæa*, *Cleodora*, *Cuvieria*, *Cymbulia*, etc., frequent the warmer waters.

The abyssal fauna, living under uniform conditions, is widely distributed, and cannot be broken up into provinces, since identical species will occur either in northern and southern parts of the same ocean or in several different oceans.

A few of the shore Mollusca are very widely distributed, such as the Common Mussel (*Mytilus edulis*)

and *Saxicava* (Plate XIX., Fig. 14), but the majority are more or less restricted, and are governed in their geographical distribution by the physical characters of the coastlines, by climate, and by currents.

They are generally considered to be capable of apportionment into nineteen "provinces," according to the abundance of peculiar forms in each. Although these provinces by no means strictly conform to the parallels of latitude, they nevertheless can be conveniently grouped in climatic zones, beginning in each case with those of the Atlantic Ocean, as follows (see Map, facing p. 66):

- | | | |
|----------------------|---|--|
| | | 1. Arctic. |
| North Temperate | { | 2. Boreal. |
| | | 3. Celtic. |
| | | 4. Aleutian. |
| | | 5. Atlantic. |
| Northern Subtropical | { | 6. Lusitanian. |
| | | 7. Aralo-Caspian. |
| | | 8. Japonic. |
| | | 9. Californian. |
| Tropical | { | 10. Caribbean. |
| | | 11. West African. |
| | | 12. Indo-Pacific, including the northern shores of Australia. |
| | | 13. Mexican. |
| Southern Subtropical | { | 14. Patagonian. |
| | | 15. South African. |
| | | 16. Australian, including the southern shores of Australia, with Tasmania, New Zealand, etc. |
| | | 17. Peruvian. |
| South Temperate | { | 18. Magellanic, with Kerguelen Island. |
| | | 19. Antarctic. |

Of these, the Boreal is perhaps the most peculiar, since it extends on the American side from Labrador to Cape Cod, and, crossing the Atlantic, includes the southern shores of Iceland and the west coast of Norway up to the North Cape.

When, however, it is borne in mind that at no very remote period of the earth's history there was a land barrier shutting the Arctic off from the Atlantic Ocean, it becomes obvious that the fauna that occupied the southern side of that barrier must, on its rupture, have been acted on by the contending currents of cold and warm water thus brought into contact. Hence it has in part been driven to the southward along the American coast by the cold northern waters that flow down past the western side of Iceland, and in part carried far to the north on the eastern side by the warm waters of the Gulf Stream.

It is impossible without giving long and tedious lists to adequately define the several faunas of these provinces, but it may be generally stated that such genera as—**Margarita*, *Lacuna*, *Velutina*, **Trichotropis*, *Buccinum*, **Neptunea*, *Liomesus*, **Trophon*, **Admete*, *Bela*, **Yoldia*, **Modiolaria*, **Astarte*, *Cyprina*, *Mya*, *Cyrtodaria*, and *Lyonsia*, are examples of the forms met with in colder regions, those marked with an asterisk (*) occurring in both northern and southern hemispheres, while *Nerita*, *Rostellaria*, *Pterocera*, *Cypræa*, *Septa*, *Cancellaria*, *Voluta*, *Oliva*, *Marginella*, *Harpa*, *Terebra*, *Conus*, *Perna*, *Vulsella*, *Spondylus*,

Plicatula, *Crassatella*, *Tridacna*, *Sanguinolaria*, and *Nautilus*, are more peculiar to the warmer waters.

Contrary to what has been asserted, there is no identity between Arctic and Antarctic Mollusca, although the prevailing dull appearance characteristic of Mollusca inhabiting cold waters, as it also is of abyssal kinds, may have helped to foster an imaginary resemblance and give colour to the bipolar theory. Tropical Mollusca, on the other hand, are more highly coloured, some quite brilliantly so.

The non-marine Mollusca, having far fewer opportunities for individual dissemination than the marine, whose free-swimming fry are readily transported long distances by currents, have naturally tended to differentiate to a far greater extent. The principal barriers to their dispersal are mountain ranges, deserts, and the sea. Each island of any antiquity offers its own little assemblage, and frequently its individual representative. *Thyrophorella* (*ante*, p. 23, Plate VIII., Figs. 18 and 19) is confined to the Island of San Thomé, in the Gulf of Guinea; the genus *Achatinella* to Ochu, one of the Sandwich Islands, though it is doubtful if, as stated, each valley has its peculiar species; while closely allied forms occur on the neighbouring islands of the group. *Cerion* is a well-known West Indian genus, of which in the main each species is confined to some single island or group of adjacent islets, and of these shells the first described, and only species known to Linnæus, *C. uva* (Plate XIII., Fig. 17), is the sole

representative in the Island of Curaçoa. Many of the Mediterranean islands have also each their distinctive shells.

Lakes that have long been isolated similarly furnish instances of peculiar faunas. Amongst these Lake Tanganyika is the most interesting. Some of the species there have such stout shells and present such a marine facies that (with the added presence of a Jelly-fish and other creatures which it had been customary to associate with marine conditions) it is not surprising that for many years it was thought this lake must formerly have been connected with the ocean. That idea, however, is now known to be quite without justification, and the fauna to be a freshwater one that has acquired its present character during a long period of isolation.

More remarkable instances of localized habitat are those of which there are two at least in the British Islands. *Limnæa involuta* is only found in a small tarn on a mountain overlooking the Lakes of Killarney, and *L. Burnetti* occurs solely in Loch Skene (Scotland). Per contra, some of the freshwater genera, such as *Limnæa*, *Planorbis*, *Ancylus*, *Physa*, *Vivipara*, *Theodoxis*, and *Unio*, have an almost world-wide distribution.

On the whole, however, like their marine kindred, the non-marine Mollusca are capable of being divided according to the prevalence of peculiar forms into faunas occupying roughly defined areas. Thirty-one "regions," as they are called, may be recognized, and these can also be conveniently grouped accord-

ing to the climatic zones they approximately occupy, further distinguishing between those of the Old and the New World, as follows (see Map, facing):

| <i>Old World.</i> | | <i>New World.</i> | |
|---|---|---------------------------------------|---|
| 1. Septentrional | { | Circumpolar and North Temperate | 21. Canadian, including Alaskan. |
| 2. Atlantidean | | | |
| 3. Circa - Mediter- ranean | { | Northern Subtropical | { 22. Californian. 23. American. |
| 4. Central Asian | | | |
| 5. Chinese | | | |
| 6. Japanese | | | |
| 7. African, West | | | |
| 8. African, Central and East | { | Tropical | { 24. Mexican. 25. Caribbean. 26. Columbian. 27. Peruvian. 28. Brazilian. |
| 9. Malagassy | | | |
| 10. Afro-Arabian | | | |
| 11. Indian | | | |
| 12. Indo-Chinese | | | |
| 13. Indo-Malaysian | | | |
| 14. Philippine | | | |
| 15. Austro-Malay- sian, and Aus- tralian, N. of 20° S. | | | |
| 16. Austro - Polyne- sian | | | |
| 17. Polynesian | | | |
| 18. African, South | { | Southern Subtropical | { 29. Chilian. 30. Argentine. |
| 19. Australian, S. of 20° S. | | | |
| 20. New Zealand | | | |
| None | { | South Temperate | 31. Patagonian. |

(No non-marine Mollusca are known from the true Antarctic Region.)

CHAPTER V

FOOD, HABITS, ETC.

THE food of the Mollusca is quite as varied as their habit of life.

That most of the land Mollusca are vegetable feeders is only too well known, but the worst offenders are certain of the Slugs that bury by day and only emerge to their feeding-grounds by night ; while the larger kinds, that scorn subterfuge and consequently bear the onus of the blame, more frequently feed on fungi and lichens, and reject green food. Some other Land Snails prefer decomposing vegetation. The Chitons, Limpets, and holostomatous Sea Snails are nearly all vegetarians. In procuring their food these vegetable consumers rasp the surface of the plant tissues with the radula, and as they move along, feeding as they go, they leave a track behind them. The marks left by Limpets may frequently be observed on the rocks off which they rasp the small algæ, while the similar tracks made by Snails may under favourable conditions be seen on palings

or the bark of trees, etc. At times these feeding tracks present quite remarkable patterns (Plate XXVII.).

A large number of molluscs enjoy a mixed diet. Nearly all the Slugs are fond of animal food, and some will invade the house in search of fats and soap, and even milk. Many of the Helicoids, especially those allied to our own Cellar Snail (*Polita cellaria*), as well as many of the Water Snails, are also mixed feeders.

The Bivalves, too, and fixed species like *Vermetus* (Plate X., Fig. 17), *Hipponyx*, *Magilus* (Plate XXVIII., Fig. 1), and probably the adult *Rhizochilus* (Plate XI., Fig. 1), subsist on the microscopic animals and plants brought to them by the currents which their ciliary apparatus perpetually excites.

Nearly all the siphonostomatous Gastropods are carnivorous, and feed on either dead carrion or on other shellfish. The Whelks (*Buccinum*, etc.), *Purpura*, *Nassa*, and the holostomatous *Natica*, by means of an acid secretion either in the saliva or from a special gland (as in *Natica*) and the aid of the radula, will drill holes through the shells of Bivalves or the upper whorls of Gastropods, and, inserting their extensile snout, devour the animal within.

In some of those species of *Murex* that have a fringe of spines round the mouth of the shell, one spike will be seen directed inwards instead of outwards (Plate XXXII., Fig. 1). This is employed by

the *Murex* as an Oyster-knife. The Bivalve prey, generally one of the Ark-Shells, is gripped in the powerful foot of the Gastropod and its shell margins pressed against the spine till the latter is driven between them like a wedge and the valves are forced apart, when the *Murex* can insert its proboscis and devour the luckless occupant at leisure. The strange spine in a like position in *Acanthina* (Plate XI., Fig. 2) may serve a similar purpose. *Sycotypus* (Plate XXXII., Fig. 12) can grip a Venus Shell while it deliberately chips out an opening with its own shell in the margin of the Bivalve. It will also insert its own shell between the open valves of the Oyster and thus keep the Bivalve Shell open while it devours the inhabitant. *Scaphander* feeds on Bivalves, which it swallows whole, crushing them between the calcareous plates with which its gizzard (Plate III., Figs. 9 and 10) is paved. The Neomenians, Lamellariidæ, and some Nudibranchs, browse on the corals, sponges, and tunicates. The Chætoderms and Scaphopoda thrive on minute forms of animal life in the ooze and mud which they frequent.

In the open sea the Pteropods also fare off micro-organisms, while *Ianthina* (Plate XXX., Fig. 2), *Carinaria* (Plate XXVI., Figs. 20-21), and *Firola*, attack the floating Jelly-fish. *Carinaria* will also capture fish, for Mr. Martin Woodward and the writer once took from the interior of one individual

six small fish, each nearly as long as their collapsed captor.

Among Pulmonates the most remarkable carnivores are the Worm-eating Slugs (*Testacella*), which follow their prey underground. Their method of feeding is peculiar, for on coming in contact with a Worm the radula is shot suddenly out, and the victim, thus impaled on the barbed teeth thereof, is drawn slowly and irresistibly into the Slug's mouth and gradually swallowed (Plate XIV.). Other members of the group to which *Testacella* belongs, such as *Oleacina*, *Natalina*, as well as some species of *Polita* and *Rumina decollata* (Plate XIII., Fig. 24), are essentially carnivorous, feeding mostly on other Snails.

The ocean-dwelling Cuttlefishes and *Argonauta* are the most rapacious of molluscs, pursuing and devouring fish, while the Octopus from his lair in the rocks will reach out a long arm and capture fish or crabs for his meal, and the *Nautilus* will take any kind of animal bait.

Of external physical conditions the one most affecting the Mollusca is the presence of moisture. Without that, existence is for them impossible. Even the Desert Snails cannot support life without occasional refreshing showers, or moisture in the shape of dew. A smart shower after a dry period will bring the terrestrial Snails out in such numbers from their hiding-places at the roots of grass and plants as to give rise to the belief that they some-

times descend with the rain. Frequently they will anticipate a downpour and climb the bushes and trees in expectation of the coming rain. The coloration of the bodies, too, at these times is said in certain species to undergo a change.

It has been supposed that excess of moisture will produce melanism in terrestrial Mollusca, but this is far from certain; cold, and possibly the nature of their food, having apparently more to do with the phenomenon.

Given moisture, temperature seems no drawback, and they become innured to very opposite extremes, though cold affects them less than heat. For those inhabiting high latitudes cold means a corresponding diminution in the period of activity, and Snails at Point Barrow, Alaska, must remain in a state of hibernation at least nine months in the year, and this probably has more effect on the animal than the mere occurrence at times of a specially low temperature.

Some of the freshwater Gastropods can also endure great heat. *Limnæa pereger* has been taken in a hot spring in Iceland where the water reached a temperature of 40° C. ($=104^{\circ}$ F.), while 50° C. ($=122^{\circ}$ F.) has been cited for *Paludestrina thermalis* at Abano. Certain of the Land Snails can also survive great heat. A living specimen of *Helix lactea* was picked up in the Sahara, where the ground temperature was 50° C. ($=122^{\circ}$ F.).

The limits of molluscan endurance, however, are said to be a maximum of 52° C. ($=125.6^{\circ}$ F.) and a minimum of -3° C. ($=26.6^{\circ}$ F.).

Seasonal changes do not, of course, cause such slow-moving creatures as molluscs to migrate, as birds and some mammals do; but their appearances and disappearances in a given locality may generally be accounted for, as in the case of plants, by the prevalence of favourable or unfavourable conditions leading to their rapid multiplication or the converse in the area under consideration. Cephalopods, perhaps, being more capable of locomotion, may migrate along a coast, and the observed departure and reappearance of the Octopus may in part be due to this as well as to causes connected with their environment affecting their multiplication.

The extremes of seasonal changes are, on the other hand, for the most part passively resisted. Some of the more active marine forms may in very cold weather retire into deeper water, but the ordinary freshwater kinds simply burrow into the mud and pass the winter in a torpid state. On the land, the Slugs burrow into the earth and form a small chamber which they line with mucus; while the Snails bury themselves in the ground, or hide under dead leaves and vegetable refuse, sometimes singly, and sometimes, as in the case of the common Garden Snails, in colonies. The most remarkable hibernacula, or winter abodes, are, however, those formed

in sheltered positions in limestone rocks, where by frequent resort the Snails in course of years erode burrows in the stone, which in places becomes honeycombed by them. In all these resting-places they either fasten the mouth of the shell with mucus to some object or to a fellow-Snail's shell ; or, when isolated, close the aperture of the shell with a film of dried mucus to exclude the cold and retain their own moisture. This film is known as the "epiphragm," or "hybernaculum," and has usually a small aperture left near the centre as an air-passage. In very cold weather, as the animal retreats farther into its shell, it will form a second and even a third epiphragm, with a space between each. In some cases such as the Roman Snail (*Helix pomatia*), this epiphragm is impregnated with lime salts to such an extent as to make it quite a solid lid (hence the name, from *pomum*, a lid). The operculate Land Snails have, of course, only to retreat into their shell and close the mouth with the operculum.

In very hot weather (and, indeed, under any other adverse conditions) the Land Snails will similarly withdraw, and protect themselves in identical manner as against cold. Freshwater Snails burrow in the mud when the water dries up, while a *Planorbis* met with in the Bahamas, under these circumstances forms an epiphragm. Certain land operculates, belonging to the Cyclophoridæ, dwelling in Further India and Malaysia, have a peculiar provision for the

admission of air during æstivation. In some species this consists of a simple notch in the peristome close to the suture, but in others the notch becomes converted into a short-necked aperture placed a little way back from the mouth, while in yet others a distinct tube is developed, either attached to the body whorl or standing free from it.

Molluscs accustomed to hibernation or æstivation probably are longer lived than their fellows ; but as a matter of fact very few real data exist concerning molluscan longevity, which probably varies a great deal. Many of the aquatic species are annuals, some of the Nudibranchs require part of two years for their full development. The young of *Doris* and *Æolis* are born in the summer in the warm shallows near the shore, drift out to deeper water, where they pass the winter, and in the following spring return to the tidal rocks, attain their full growth early in the summer, and after spawning-time disappear. The Mussel, Cockle, and Ship-worm attain their full growth in a year, *Pteria* in two years, the Oyster in five, though in Oyster-beds it may live for ten years. The huge *Tridacna* is credited with eight years, while the Swan Mussel (*Anodonta*) is said to reach twenty or thirty, and many of the marine Gastropods probably attain a comparatively great age. The Periwinkle has been kept in captivity for nearly twenty years.

The Land Snails are mostly biennial, but the

Common Garden Snail (*Helix aspersa*) has been known to survive in captivity for nine years.

Less is known about the duration of life among the Cephalopoda, but it is said that *Rossia* does not live for more than a year, and the Octopus not more than four years.

As regards tenacity of life, many instances are on record of Mollusca surviving under very adverse conditions (see also *ante*, pp. 52, 53 and 71). Among the more remarkable the following may be cited: Specimens of *Littorina muricata* were kept out of water for a whole year and then found to be alive. A Pond Mussel was sent to Dr. Gray from Australia that lived 498 days after it was taken from the pond, having in the interim been only twice in water to see if it were alive. Some specimens of *Ampullaria* purposely placed in a drawer in Calcutta were found alive after five years, despite the warm climate.

Those molluscs, however, which are most accustomed to "summer sleep" seem to come off best, and Land Snails will stand months and years of close confinement without food.

A specimen of *Helix Veatchii*, from Cerros Island, is said to have existed without food for six years. The most striking instance, perhaps, is the well-known one of the specimen of *Helix desertorum* from Egypt, that was stuck down on a tablet in the British Museum on March 25, 1846, and found on March 7, 1850, to be alive: released and revived, it lived in

confinement through two summers, became torpid in October, 1851, and was found to be dead in May, 1852. This specimen (Plate XIII., Fig. 34) was figured by Dr. S. P. Woodward in his "Manual of the Mollusca." The Rev. A. H. Cooke collected examples of this species in Egypt in 1904, and kept them in a tin box without food. In January, 1912, ten individuals were still alive, but only three survived by the following March, although food had been supplied to them.

There is a record in the Philosophical Transactions for 1774 of some Snails that had lain by in a cabinet for more than fifteen years resuscitating on being placed in water ; but, despite the detailed statement and assertion that no error was possible, the narrative does not seem credible.

Such dainty morsels as molluscs are naturally relentlessly pursued and devoured. Leaving man out of the question, many animals from the Whale to the Mouse prey on them.

A Monkey (*Macacus cynomolgus*) has been seen to feed on Oysters, the shells of which he broke open with a stone. The Right Whale devours enormous quantities of Pteropoda with other pelagic creatures ; the Cachalot, Grampus, and other Cetacea, devour Cuttlefish. The walrus digs Bivalves out of the silt on the sea-floor with his tusks, and eats them. Otters, Badgers, Raccoons, an Ichneumon, various Rats and Mice, as well as Hedgehogs and Shrews,

and even the Coyote, will feast on them. Very many birds besides the Thrushes¹ partake of Land Snails; while Sea-Gulls and other sea-birds, with Crows, will forage at low water for the marine kinds; and sometimes, carrying them inland to devour, will drop the shells in places where they may well puzzle future geologists by their presence. Swans, Ducks, Geese, and other water-birds feed on freshwater Mollusca, especially the young ones. Slow-worms are very fond of Slugs; Frogs and Toads less so; Newts will take freshwater Snails. Fish, especially marine ones, consume large quantities. The Cod, Gurnard, Wolf-fish, even the Mullet and Sole, to name a few, make their diet off Bivalves; while the Conger will attack and devour the Octopus.

Among invertebrates their worst enemies are their own kindred, as already noted. Crabs will break open the shells of young Oysters to get the animal within. Certain insects seem to select Snails for their victims. The female Glow-worm (*Lampyrus noctiluca*) attacks and kills *Helix nemoralis*. *Staphylinus olens* has been seen to set upon and kill the Heath Snail (*Helicella itala*); and the larva of another Beetle, *Drillus flavescens*, will even assault a land operculate (*Pomatias*), watching till the Snail begins to issue forth, and then with its strong jaws

¹ Though Blackbirds are commonly credited with also eating Snails, it is very doubtful if they really do, especially the larger kinds.

cutting the muscle that attaches the operculum to the animal to prevent its closing, after which it proceeds to devour the animal and undergo its metamorphosis within the shell. Some species of *Silpha* seize small *Helices* in their mandibles, and break the shell by throwing their head back and striking it against their prothorax. The larvæ of *Cochleoctonus vorax* prey on different species of Snails. The big Water Beetle (*Dytiscus*) and other water insects live largely on Water Snails. To what extent larvæ of Flies thrive on living Snails does not seem quite certain. *Melanophora helicivora* appears to be parasitic in France on *Helicella conspurcata*. In North America *Sarcophaga heliis* has been bred from *Polygyra thyroides*, and *Cynomyia mortuorum* from dead Snails. *Wandolleckia achatinæ* has been found running over living *Achatina* in Liberia, but whether they are parasites or not does not appear.

Small molluscs are swallowed whole and the animal digested out by Sea Anemones and Starfish. The latter, too, is very destructive in Oyster-beds, opening the valves either by main force or other means, and then, everting its stomach and passing it between the valves, it digests and absorbs the mollusc.

Among molluscan parasites the most abundant belong to stages in the development of Platyhelminthian Worms, which complete the cycle of their existence in some other animal, such as Birds, Fish, Frogs, etc. The history of these is completely

known in but a few cases. Thus, the sporocyst of *Distomum macrostomum* is found in the tentacle of *Succinea*, and completes its development in the Bird that swallows the Snail. The early stages of the Liver Fluke of Sheep (*Distomum hepaticum*) are passed in the body of *Limnæa truncatula*, which lives on the margins of ditches and small streams, and after floods may be left stranded on the surrounding herbage. Sheep feeding near such spots are apt to take in the Snails with their food, and so become infected. Still more interesting is the fact that the pearl of commerce has been said to owe its existence to the action of a Cestode larva (*Tetrarhynchus*), which completes its life-cycle in the bodies of two successive kinds of Fish that prey—the one on the Pearl Oysters, the other on its fellow, as well as on the Oysters. The supposition is that, if the embryo worm, on forcing its way into the tissues of the mollusc carries with it some of the epithelial cells of the latter, an abnormal growth of pearl-secreting cells within the tissues of the animal results, and a pearl is formed, having the parasite for its central point.

Some of the Nemertine Worms are also parasitic on Mollusca, while certain Leeches are likewise known to attack them.

The relationship in the foregoing cases is undoubted, but in other instances it may be merely a case of commensalism. Thus, several small Crus-

taceans of different sorts (*Ismaila* and *Splanchnotrophus*) are to be found on Nudibranchs; another attaches itself to the float of *Ianthina*, which it matches in colour. *Ostracotheres* lives in the gills of the Giant Clam (*Tridacna*); while *Pinnotheres* takes up its abode within the shells of several different Bivalves, including the great Pearl Oyster, and one species has lately been found in *Strombus*.

A quaint little Mite (*Philodromus limacum*) infests terrestrial Gastropods. It lives in the breathing chamber, and may be seen issuing therefrom and running with great rapidity over the body of its host, but what its connection with the mollusc may be is quite unknown. Another kind of Mite (*Atax*) is found on freshwater Mussels.

Clear cases of commensalism on the part of molluscs with other animals are those of certain of the Pelecypods: *Modiolaria marmorata* lives in the integument of Ascidians; *Montacuta*, *Lepton* and *Scioberetia* dwell with Echinoderms. *Jousseaumia* is commensal in the chamber of a Sipunculid Worm (*Aspidosiphon*), which is itself commensal in the coral genera *Heterocyathus* and *Heteropsammia*. *Lepton squamosum* resides in the burrows of Annelids and Crustaceans; *Ephippodonta* is commensal in the burrow of a Prawn; *Vulsella* lives in the substance of Sponges. The Gastropod *Magilus*, which takes up its abode in coral masses, and probably supports itself on the Infusoria and other small animals which

the coral polyps draw towards themselves by their ciliary action. So, too, probably do its close relatives *Coralliophila*, *Leptoconcha*, and *Rhizochilus*. The last named in its adult state attaches itself to the branches of *Antipathes*, and all but closes the mouth of its shell (Plate XI., Fig. 1).

Some of the Bivalves, which bore into coral, such as *Coralliophaga* and *Lithodomus*, may also similarly profit by their situation.

Whether the occurrence of the small *Planorbis*-like *Cochliolepis*, which was found in Charleston Harbour under the scales of the Annelid (*Acoëtes*), was a case of commensalism or parasitism has not yet been made clear.

Several molluscs are themselves parasitic on other creatures: Starfish and Echinoderms are peculiarly liable to these parasites. *Stilifer* (Plate XXVI., Fig. 27) and *Robillardia* nestle among the spines of Echinoderms, while both the former and *Stiliferina* occur buried in the skin of Starfish, and *Thyca*, one of the Capulidæ, attaches itself to the under side of the rays. These feed on the juices of their host, which they absorb through the long proboscis they insert into their victim. The Sea-Cucumbers come even worse off, for not only are they thus similarly attacked from without, but afford lodgment within to a variety of blood-suckers—viz., *Entovalva*, a Bivalve; *Eulima* (Plate XXVI., Fig. 26), a relative of *Stilifer*; and a series of other Gastropoda, *Ento-*

concha, *Entocolax*, *Entosiphon* and *Enteroxenos*, etc., whose exact relationships are unknown, and whose appearance, so transformed are they, suggests almost any vermiform animal rather than a Snail. One instance has also lately been placed on record of a mollusc (*Epistethe gonodactyli*) parasitic on the ventral surface of a Stomatopod crustacean (*Gonodactylus chiragra*) from shallow water in the Persian Gulf.

A more interesting form of parasitism is afforded in the early life-history of the freshwater Mussels, and it is said in that of the marine Bivalve *Philobrya* also. The young Mussels are hatched between the gill-folds of the parent, and, having passed there through the veliger stage, escape through the ex-current siphonal opening in the form of a peculiar larva, which when first observed, being thought to be a distinct creature, received the name of *Glochidium* (Plate XXIX., Fig. 9). This larva has a hook in the middle of the margin of each of its two valves, which, moreover, are perforate, and also a long byssal thread. It is incapable of supporting an independent existence, and cannot, as has been stated, swim by rapidly opening and closing its valves. This valve-clapping takes place vigorously if a fish comes near, and has the effect of forcing the byssus straight out. Should the latter touch the fish, it adheres to it. Any chance movement then bringing the *Glochidium* itself into contact with the fish it immediately snaps to. The hooks, if the part

seized be a soft portion such as a fin or a gill-filament, penetrate the tissues, and the irritation they set up causes an overgrowth of the skin of the fish to envelop the Glochidium, which thus cradled thrives for some two to six weeks on the juices of its host. Meanwhile the byssus and adductor muscle of the Glochidium disappear and the two permanent adductors of the adult and the foot are developed. The mantle secretes a new shell, resembling the adult form, beneath the Glochidium shell, which persists, however, for three or four weeks after the young Mussel is again set free by the perishing of the containing cyst. By the time, though, that it quits this temporary abode and proceeds to complete its growth, it has almost certainly been carried far from the place of its origin to some spot where perhaps there will be more room for it.

Overcrowding is undoubtedly as bad for animals as it is for plants, and in the vegetable kingdom various well-known adaptations are provided to insure the dispersal of the seeds and their conveyance to fresh soil. Among the Mollusca the instance just cited is perhaps the most distinct example of a like provision. With the marine Mollusca the shifting waters of the sea are practically the sole vehicle for the transportation of the young to new spots, and the embryos of nearly all, including those that, like the Oyster, are fixed in the adult state, are free swimmers, principally on the surface of the sea.

Nevertheless, when such millions of fry are produced by even a single parent (see *infra*, p. 89), and all committed to a sole agent for dispersal, it is evident that the greater number will be carried in one direction and to a single area, and that the shorter the time before they settle down the greater will be the number thus congregated together. To this fact must be attributed the large assemblages of one species, such as the Common Shore Mussel, and not to any wish for a gregarious or social life after the manner frequently displayed by animals higher in the scale of organization. To their limited capacity for locomotion is similarly attributable the colonies of Land Mollusca. Each lives for itself, competing with its fellows for food, the abundance or dearth of which principally determines their numbers, without thought of co-operation or mutual assistance.

What the currents will effect for marine Mollusca, the running water of streams and rivers, especially in times of flood, will do for the freshwater ones and more, since during floods not merely the eggs and offspring, but the animals themselves, will be borne away to fresh spots by the rushing current, and, as the waters subside, be left in ponds and ditches that are otherwise disconnected. The colonization of permanently isolated pieces of water, and even the dew-ponds on high hills, apart from accidental importation by man, is effected by other agencies of

dispersal. Not infrequently large Water Beetles have been captured in flight from one piece of water to another that have proved to be carrying molluscs attached to them. It may be one or more Bivalve Shells holding tight on to the legs, or a freshwater Limpet (*Ancylus*) or two, adhering to the wing-cases. The fry of other kinds of Snails may be readily transported in similar fashion. Water-fowl and Wading Birds have likewise been taken with Bivalves adhering to their feet, and have been observed to fly off with water-weeds clinging to them that might well bear both small kinds of shells and ova. Young Snails may also be transported sticking to the bird's plumage. On the arrival of the insect or bird at a fresh piece of water these involuntary passengers drop off, and in this way fresh colonies are started.

Land molluscs and their eggs adhering to vegetation are carried down by flood waters and stranded on subsidence in fresh pastures. Small forms dwelling in swampy ground and ova may furthermore be conveyed to distances in the mud sticking to birds' feet, or clinging to their feathers, especially if the birds be such as roost on the ground.

Transport by man, both intentional and accidental, hardly enters into consideration here; but it is interesting to remark how the commoner and hardier European Slugs and Snails have been introduced near ports of call in many widely separated

parts of the globe, such as the Cape and Australia. Probably, too, the uniform distribution round the shores of the Mediterranean of the commoner sorts is due to the existence of trade in the area from very early times.

CHAPTER VI

REPRODUCTION

THE sexes in the majority of the molluscs are separate. Hermaphroditism accompanies specialization, and only obtains normally in the Neomeniina among the Amphineura, the Euthyneura and some genera of Streptoneura among the Gastropoda, the Anatinacea, and a few other isolated instances among the Pelecypoda.

In those forms in which the sexes are separate there is often a definite sexual dimorphism. Frequently the female is the larger and the more tumid, as in *Littorina*, *Vivipara*, and the British land operculate, *Pomatias elegans*; while in *Lacuna pallidula* the female outweighs the male by ten to one. Differences are also exhibited in the mouth of the shell in *Littorina obtusata*, in the operculum in some species of *Cerithium*, in the teeth of the radula in *Nassa*, while in *Vivipara* the right tentacle of the male is curiously modified.

In the Pelecypoda dimorphism is recognizable in

Unio batavus, *U. tumidus*, and *Lampsilis*, in which the female is rather broader than the male, and in *Astarte*, in which the border of the shell is smooth in the male, but crenulated in the female.

Among the Cephalopoda sexual dimorphism is very marked, especially in the Argonaut, the female of which may attain to fifteen times the length of the male. Generally the males are more slender than the females, but in *Nautilus* the hood of the animal and the mouth of the shell in the male are wider than in the female. The male Cuttlefish is also remarkable for the curious modification of one of its arms, known as "hectocotylyzation" (Plate XXV., Fig. 14). At the time of pairing this arm becomes charged with the spermatophores, and is the vehicle for their transference to the female. In some cases—as, for example, the Argonaut—the hectocotylus becomes detached from the male and is able to live and move about for a considerable time. It has even been described as a parasite on the female.

Most of the Mollusca are oviparous—that is to say, lay eggs; in a few cases the eggs hatch within the body of the parent, and the young are brought forth alive, as in *Calistochiton* among the Amphineura, *Melania* and *Vivipara* (Plate II., Fig. 7) among freshwater Gastropods, *Cymba* and many species of *Littorina* among marine; several isolated instances also occur among the land Pulmonates—e.g., *Pyramidula*, *Opeas*, some Pupillidæ, etc. In the

Clausiliidæ the eggs are also sometimes extruded before hatching, as happens in *Balea* (Plate XIII., Fig. 18) and some species of *Clausilia* itself.

The eggs are isolated in the Amphineura, the more primitive Gastropoda, in the Scaphopoda, and the Pelecypoda. In the majority of the aquatic Gastropoda they are either enclosed in tough capsules, which may be deposited apart (as in *Purpura*), or in irregular clusters (as in the Whelk, Plate XXX., Fig. 3). Or the spawn consists of large numbers of eggs agglutinated in gelatinous masses, or spread out in the shape of a strap or ribbon, in which the eggs are arranged in rows. This "nidamental ribbon" is sometimes coiled up like a watch spring and attached by one of its edges (*e.g.*, *Jorunna Johnstoni*, a Sea Slug, Plate XXX., Fig. 4). The nidamental capsules of the Cuttlefish are clustered like grapes, each containing but a single embryo. In *Ianthina*, the purple Sea Snail, the egg capsules are carried closely packed on the under side of a raft or float, formed by the parent, and attached by one end to her foot (Plate XXX., Fig. 2).

The number of eggs laid at a time varies in the different species, but is greatest in the Pelecypoda.

The Swan Mussel (*Anodonta cygnæa*) has been computed to lay from 14,000 to 2,000,000; the Painter's Mussel (*Unio pictorum*) 220,000; the Common Oyster from 600,000 to over 1,800,000; while a large American Oyster may, it has been said, contain more than

100,000,000 ova. A portion, supposed to be one-seventh of the ovary of a Ship-worm (*Teredo*) was estimated to contain 1,874,000 eggs. For Chiton 200,000 is quoted. Among Cuttlefish *Loligo* and *Sepia* are said to have 30,000 to 40,000. A single nida-mental ribbon of the Sea Slug (*Archidoris*) has been reckoned to enclose 50,000 to 300,000. The single capsules of *Purpura lapillus*—and one individual, it is said, has been observed to produce 245 of them—contains from 400 to 600 eggs, of which, perhaps, only 10 to 16 attain maturity, the remainder serving as their food while in the capsule. The Pulmonata lay comparatively a small number of eggs. The freshwater Limpet (*Ancylus*) lays only 5 or 6, *Limnæa* and *Planorbis* 20 to 100 in each mass. The common Garden Snail (*Helix aspersa*) produces 40 to 100. The viviparous forms average fewer, *Vivipara* bringing forth about 15, and the Stenogyridæ about 4 or 6. The eggs of many of the Land Snails have a regular calcareous shell, and are sometimes of great size, those of the African *Achatina* and the South American *Strophocheilus* (Plate XXX., Fig. 1) rivalling a pigeon's egg in magnitude.

In most cases the eggs or young are at once abandoned to their fate, but in some instances a partial protection is extended to them in their early stages. Occasionally the eggs are attached to the parent shell. This is the case in *Liomesus Dalei*, while several species of *Theodoxis* and *Septaria* have

a similar habit. Among these "incubatory" forms is *Calyptræa Chinensis*, whose egg capsules are retained between the foot of the parent and the object to which it is attached. *Vermetus* retains them within the mouth of the shell. The female Argonaut secretes and carries about a shell as already described (*ante*, p. 40) solely for their protection. Her eggs, in a granulated mass attached to a many-branched stem, are retained in the spire of this nidamental shell. Another Cuttlefish (*Polypus Digueti*) on the Californian coast, failing a shell of its own, makes use of the empty tenement of a large Bivalve. In this it establishes itself, facing outwards from the hinge, and by means of its arms opens and closes the shell at will. It deposits its eggs round about in the under valve, and the young, as they successively hatch out, swarm about and crawl over the parent, who remains ready to shut the shell at the first sign of danger.

Certain small Land Snails belonging to the group *Libera* of the genus *Endodonta*, met with in the Antipodes, deposit their eggs in the umbilicus of the shell, sealing the opening with a thin, sometimes shelly, epiphragm, through which on hatching the young perforate their way.

In some species of *Melania*, *Spekia*, and *Tanganyicia*, the embryos develop in a special brood-pouch formed by an infolding of the skin near the right tentacle.

It is among the Bivalves, however, that the most

abundant instances occur of incubatory retention of the young, usually in the spaces between the gill-folds. The freshwater Mussels (*Unio*, *Anodonta*, etc.) and the little freshwater Bivalves *Sphærium* and *Pisidium* are noted examples; in the two last-named instances there are special brood-pouches for the reception of the newly hatched young. In the freshwater Zebra Mussel (*Dreissensia*), on the other hand, the young are launched out at once into the water. Among marine forms retaining the brood are *Arca vivipara*, *Philobrya*, the Oyster, which keeps them in the mantle, and the Ship-worm (*Teredo*) which houses them in the gill chamber, while in one Bivalve, *Thecalia concamerata*, the female forms a shelly chamber within the margin of the shell for the reception and protection of the young.

The early stages in the development of the young Mollusca are the same as in all other animals. The original cell splits up into many cells, until the resulting mass looks like a mulberry. The constituent cells, however, are unequal in size, one series, the first formed, or macromeres, being larger than the others, or micromeres, and almost surrounded by them. This disparity in size is less marked in primitive forms like the Limpet, but most pronounced in the Cuttlefish, in which the macromeres are most highly charged with food-yolk. In the Gastropod ovum it is interesting to note that a curious obliquity in the cleavage becomes evident,

known as the "spiral cleavage," and that this obliquity takes a reverse inclination in sinistral forms to that which obtains in dextral.

In the succeeding stage of the development the macromeres, which have undergone further subdivision, form the inside lining of the mulberry, as it were, and enclose a cavity which ultimately becomes the digestive tube. Other cells arising between the layers of micromeres and macromeres subsequently form the various organs and muscles of the young animal. Meantime there arises a swimming organ called the "velum." It begins as a ridge fringed with fine hairs (cilia) encircling that part of the head of the embryo which lies in front of the mouth, and it finally expands into a sort of disc, which is drawn out into lobes or into fingers. This condition is the "veliger stage," which, as already remarked, is characteristic of the Mollusca (Plate XXIX., Figs. 1-8). The stage is further marked by the formation of the young shell and the first appearance of the foot. As the young mollusc grows up the velum disappears.

Many larval forms, especially among the Gastropoda, are very different from the adult both in the appearance of the animal and the shell, and have been described as distinct species, while the adult form of some has not yet been ascertained. Thus the young shell of *Lamellaria* has received the names of *Brownia*, *Calcarella*, *Echinospira*, etc., while *Mac-*

gillivraya (Plate XXVI., Fig. 29) is probably the young of *Dolium*, and under the name *Sinusigera* (Plate XXVI., Fig. 28) a large number of the young of very different genera has been included.

To the curious parasitic (glochidial) stage of the young freshwater Mussels and *Philobrya* that succeeds the veliger stage allusion has already been made (*ante*, p. 82).

There is usually a marked difference between the embryonic shell ("protoconch" of Gastropods, "prodissoconch" of Pelecypods) and the adult, the junction between the two being very marked, and indicating a pause in the growth of the shell, during which time the young animal was completing its growth in other respects (Plate IV., Fig. 2; Plate XXIX., Figs. 14 and 15).

The Gastropod shell in the very early stages of its formation is exogastric—*i.e.*, coiled forward over the head of the animal (Plate IV., Fig. 1, C)—but it speedily takes on the right or left spiral of the adult. Even in the Limpet (*Patella*) and Keyhole Limpets (Fissurellidæ) in their embryo stages have coiled exogastric shells. The Fissurellidæ are further interesting in that the characteristic perforation, beneath which the posterior termination of the alimentary canal lies, first appears as a slit in the margin of the young shell. In *Emarginula* (Plate VII., Fig. 1) the slit persists through life, the hinder end being constantly filled up as the animal grows;

but in *Rimula* (Plate VII., Fig. 7) the anterior portion of the slit is bridged across with shelly matter when the animal is half grown, and the quondam slit remains as a perforation half-way between the apex and margin of the shell. In *Fissurella* the same thing takes place quite early in the animal's history, and the resulting perforation is left almost at the apex of the shell (Plate XXIX., Fig. 14). The series of holes in the shell of the Ormer (*Haliotis*, Plate VII., Fig. 8) have a similar origin, the perforations resulting from a periodic bridging of the marginal slit during the creature's growth. In *Schizodentalium plurifissuratum*, on the other hand, the perforations have been subsequently drilled, for there are more slits in the adult than in the young shell, and it is the habit of the Scaphopoda to absorb the apex of the shell in proportion as the aperture is added to. The very young shell of *Dentalium* (Plate XXIX., Fig. 6) is so deeply cleft as to be almost bivalve.

A somewhat analogous parallel to *Fissurella* is offered in the common Bivalve *Anomia*. The adult shell is attached to various objects by the strong shelly byssus which passes through a circular notch near the umbo of the flat valve. When quite young, the little shell has no such opening, but after it has attached itself and begins to increase in size, the margin of the flat valve literally grows round the byssus, leaving the characteristic orifice, which, as the shell enlarges while it remains stationary, appears

proportionately nearer and nearer the umbo (Plate XXIX., Fig. 15).

Another interesting instance of change in growth is afforded in the fossil *Velates* (Plate XXXII., Figs 1-6). This, when young, closely resembles a *Theodoxis* (= *Neritina*) in appearance, and, like it, grew spirally. When about half an inch in diameter (*i.e.*, when about four and a half whorls have been completed), however, it ceased to grow spirally, and continued the lip of the aperture in an oblique outward direction, depositing at the same time copious shelly material on the columellar wall of the body-whorl, while it obtained the extra room required within by reabsorbing the inner side of the shell at that point. In the end the adult animal is seen to have occupied a single chamber excavated in previously deposited shell—a unique example of most uneconomical molluscan architecture.

In most embryo Gastropods an operculum is present, though subsequently frequently discarded (Plate XXIX., Fig. 5, o). The Pulmonata (except the Auriculidæ, Siphonariidæ, and Oncidiidæ, which have an operculum during development, and *Amphibola*, which retains it throughout life) do not develop an operculum; furthermore, the veliger stage is reduced or altogether wanting in the members of this order, as it is in viviparous species whose young are hatched in the adult condition. In those Gastro-

poda which are naked when full grown, the shell falls off soon after the reduction of the velum.

With the arrival of adult characters come the characteristic markings and sculpturing of the shell, with its concomitant adornment of spines and processes when such are produced in the course of growth. In some forms, like the Unionidæ, the young shell is at first wrinkled, becoming smooth in later life, and a similar loss of sculpturing is observable in some Gastropods (*e.g.*, certain species of *Rostellaria* and *Fusus*) as well as some Ammonites.

Arrived at maturity, the final features of the fully formed shell are assumed. The young Cowry shell (*Cypræa*) has a thin, sharp lip (Plate XXVI., Fig. 30), which becomes curled inwards and enormously thickened and toothed in the adult (Plate V., Fig. 5). The Scorpion Shell (*Pterocera*, Plate V., Fig. 11), *Strombus* (Plate VIII., Fig. 3), *Rostellaria* (Plate X., Fig. 20), *Aporrhais* (Plate II., Fig. 3), and others, develop the curious spines and projections that surround the mouth. *Rhizochilus*, as already noted, attaches itself to the *Antipathes*, and almost entirely closes the mouth of its shell (Plate XI., Fig. 1). The Land Snails form a thicker lip or narrow their aperture with projecting processes, so that it is a marvel how they pass in or out, and how they can exclude their eggs (Plate VIII., Figs. 14-16).

In some other Gastropods the final whorls become more or less uncoiled as in *Diaphora tuba* (Testacellidæ), *Brachypodella Brooksiana* (Plate XXXII., Fig. 10) belonging to the Urocoptidæ, in *Hypselostoma*, and other Land Snails, as well as among marine species such as *Vermetus* (Plate X., Fig. 17) and *Tenagodes* (Plate V., Fig. 8); whilst in *Blæospira echinus* the whole shell is scalariform. Then, again, the aperture may be turned upwards towards the spire, as in *Anostoma* (Plate XIII., Fig. 31) and *Hypselostoma*; while the last whorl may be carried right up and over the spire, as in certain species of *Opisthostoma* (Plate XXXII., Fig. 7). In *Gibbus* the body whorl is flattened and curiously constricted at one point, as if the shell had been made soft and then pinched up (Plate XXXII., Fig. 8).

Some Bivalves continue to increase the thickness of their shells by additional deposition to the inner layer long after they have ceased to grow outwardly. This is especially noticeable in the Oysters, *Gryphæa arcuata* (Plate XXX., Fig. 5), *Spondylus*, and other attached forms. In the case of *Ostrea cornucopia* and *Spondylus varius* (Plate XXX., Fig. 6) the added shelly matter is not solid, but full of cavities filled with fluid. *Pholadidea*, a close relative of the Piddock, or *Pholas*, fills up the anterior opening of the valves with a callous plate. The Ship-worm (*Teredo*) and some other borers are said to close the end of their burrows when adult. In *Nautilus* the last

chamber is proportionately shallower than the rest (Plate I.). The fossil Ammonites frequently exhibit great changes in the course of growth, so much so that the different stages have been mistaken at times for distinct species.

CHAPTER VII

EVOLUTION

THE study of evolution in the Mollusca is an exceedingly complex one. Their extreme plasticity naturally renders them both peculiarly susceptible and readily responsive to the operation of the two great factors that govern the lives of all animals—namely, the influence on them of their environment and the necessity laid on one and all of procuring food. The molluscan mode of life is, in fact, mainly governed by the combined action of these two controlling influences, and in turn itself becoming a potent factor, completes the cycle by reacting on the animal, which is thus impelled, so long as similar conditions hold, yet further along a given line of development.

Owing, however, to the paucity of stable elements to be acted on, continuous progress in any direction has, despite the antiquity of the race, been slow indeed. The total lack of anything like internal framework has militated against any such wonderful

progress as exhibited in the vertebrate kingdom; the very plasticity of these creatures has thwarted progressive development, as we understand the phrase, and they readily retrograde, or branch off, into bypaths. Nevertheless, progressive development is traceable in certain characters, while in other conspicuous features the action of environment or individual requirement alone seems responsible.

It will suffice to take certain leading features and organs to summarize what is known concerning them, and to point out what conclusions, if any, can be based upon them.

The tidal zone was in all probability the cradle of the race, although it has been argued by some with much show of reason that the earliest forms were pelagic. From the shore the various members betook themselves, mostly to deeper and deeper water on the one hand, but also, though perhaps more tentatively and gradually, to fluviatile and terrestrial conditions on the other.

Now, the first requirement of a soft-bodied animal, and especially of one considered by its fellows to be good eating, is protection. In early days, however, enemies were far fewer than now, and it was rather from the force of the elements that preservation was needed.

This first requirement is supplied by the shell, and all three types, Univalve, Bivalve, and Multi-

valve, made their appearance early in the history of the race.

The last named, the Chitons, first occur in the Ordovician (*Priscochiton*). They are, however, a conservative race, and have not materially changed their form since those far-off days. Still, taking the Amphineura as a whole, the class shows a desire to disburden itself of its coat of mail.

Through the successive genera of one branch of the Polyplacophora (*Acanthochites*, *Amicula*, *Cryptochiton*, and *Cryptoplax*, Plate IX., Fig. 3) the component plates become wider and wider apart, and the whole animal more vermiform, while in the worm-like Aplacophora (Plate IX., Figs. 4-6) the shell has disappeared, though numerous calcareous spicules remain scattered over the mantle.

As regards the Gastropoda, when it is borne in mind that the embryonic shell is nautiloid and exogastric, and allowing for the Gastropod peculiarity of spiral torsion, the number and variety of forms assumed in the adult state is remarkable. Seeing that departures from this embryonic, and therefore primitive, type are pronounced, even in the earliest known Gastropods, it is not possible to say how far environment or other forces may have played part in their development. Certain elongate forms of shell like that of *Terebra* (Plate XII., Fig. 5) would seem a positive disadvantage to the animal. Nevertheless, certain broad characteristics are observable.

Primarily among the inhabitants of a rough fore-shore the massive strength of the shell is noticeable, the object being, of course, to withstand the battering action of the waves and hard substances like stones cast up by them.

To this end the conical form of the tests of the Limpets (*Patella* and *Fissurella*) is admirably adapted, hence the recurrence of this particular shape in widely different molluscs. Thus it reappears in the Capulidæ, a family dating back in time as far as do the Docoglossa; in the Hipponycidæ; in the freshwater Limpets (*Ancylus*, *Acroloxus*, etc.), which in swift-running waters are liable, only in a lesser degree, to the same troubles as the marine surf dwellers; and more strikingly still in those Pulmonates that have reverted to the marine surf as a habitat (*Siphonaria*, Plate XXVI., Fig. 24; *Gadinia*, Plate XXVI., Fig. 25; and *Aporemodon*). The pateloid shape is also approximated in the freshwater genus *Septaria*, an operculated form allied to *Theodoxis*, but in which the operculum, being no longer in use, since the animal cannot retire into its shell, is reduced in size and buried in the substance of the foot; while a parallel instance in a widely different animal dwelling under similar conditions is afforded by the familiar Barnacle.

The early spiral Rhipidoglossates seem mostly to have had stout shells; certainly this is the case with the modern Neritidæ, Turbinidæ, Trochidæ, and

their kindred. Most of the members of these groups are furnished with thick opercula, which are not withdrawn far within the mouth of the shell. With the capacity, however, for retreating further and further into the shell, and so out of the more immediate reach of danger of violent injury, the operculum, always an encumbrance, tends to become less and less ponderous.

Other inter-tidal forms belonging to families higher in the molluscan scale have also, under the necessity of facing similar conditions, developed strong shells; such are *Littorina*, *Purpura*, *Nassa*, and, among tropical genera, *Pterocera*, *Turbinella*, and *Strombus*. The last named, indeed, is the most difficult of all shells to break, resisting even the lusty application of a geological hammer.

When, however, the foreshore is quitted in favour of deeper water, where no surf breaks, and where the sea-bottom is composed of soft sand or silt, a ponderous shell ceases to be essential for protective purposes and becomes a positive disadvantage in locomotion. This drawback is further increased in the case of Gastropoda that are carnivorous, as the higher forms mostly are, for even the slow-moving Bivalves on which they feed require greater activity to seek out and capture than does a rooted plant. Hence the reduction in shell and operculum shown by the inhabitants of the laminarian as contrasted with those of the littoral zone.

The process continuing as specialization proceeds, the shell ever tends to decrease in size till it remains solely as a protector for the more vital organs as in the Tectibranchs (Plate XII., Figs. 14-19), or disappears as in the rhipidoglossate *Titiscania* and the Nudibranchs (Plate XII., Figs. 20-28).

A similar reduction and disappearance takes place among the pelagic forms. Light as *Ianthina* shells are, they are substantial compared to the glassy films carried by the Heteropods (Plate XXVI., Figs. 17-22) and shell-bearing Pteropods (Plate XXVI., Figs. 1-9), while *Phyllirrhoë* and the shell-less Pteropods (Plate XXVI., Figs. 10-16) have discarded all covering whatsoever.

The freshwater Gastropoda, save those few that inhabit turbulent waters, have, as might be expected, thin shells; but though *Amphipeplea* (Plate XIII., Fig. 5) and *Physa* (Plate XIII., Fig. 7) tend to overflow their shells, an absolutely shell-less example remains to be discovered.

On land heavy shells are certainly at a discount, and though some such occur among the Auriculidæ, in certain species of *Strophochilus*, in *Leucochroa* (where it serves as a protection against extreme heat), and many of the Cyclophoridæ; still, viewed broadly, the tendency, as might be expected, is to a lightening and diminution of the shell to the point of disappearance, and this more especially in the carnivorous and semi-carnivorous forms. In fact, nearly all the families of

Land Snails culminate with highly specialized representatives, in which the shell is not only extremely dwarfed, as in many well-known instances, but is reduced to an internal vestigial plate, as in *Chlamydothorus* (Testacellidæ), *Limax* (Plate XIII., Fig. 12), and allied genera (Limacidæ); *Metostrecon* (Helicidæ); *Hyalimax* (Succineidæ ?); and *Athoracophorus*; or to mere granules as in the Black Slug (*Arion*); while it is totally wanting in *Trigono-chlamys*, *Pseudomilax*, *Philomycus*, *Veronicella*, and *Oncidium*.

The Scaphopoda have not materially altered their habits from the first, and the function of the shell is merely to protect the soft parts from the lateral pressure of the surrounding silt, and to that end the tubular form is most suited.

Among the Pelecypoda the shore-frequenters of the older and, broadly speaking, less specialized types exhibit on the whole stouter and more convex shells than the later and more specialized ones. Especially stout are some that have, like the Giant Clam (*Tridacna*) and the Bear's Claw (*Hippopus*, Plate XIX., Fig. 5), to withstand the full beat of ocean waves; so, too, are those of the fossil reef-builders of the *Rudistes* (Plate XIX., Fig. 7) group.

The most primitive form, *Nucula* (Plate XVII., Fig. 1), that has come down to us from palæozoic times is without siphons or byssus; but some species of its near ally, *Arca* (Plate XVII., Figs. 5 and 6), which boasts an equally long ancestry, have attained the

faculty of mooring themselves by a byssus and so defying the waters. *Mytilus*—the Common Shore Mussel—which also comes of a family having a long pedigree, has not a particularly stout test capable of resisting heavy blows, but it meets the waves with its outwardly directed, sharp, wedge-shaped shell and cleaves them instead; while it does not settle, or perhaps to speak more accurately, does not establish itself in spots where it would be liable to damage from stones thrown up by the sea.

Most of the Bivalves, as a matter of fact, do not live in exposed situations, but burrow more or less deeply into soft sand or silt. Here those that do not penetrate to any depth below the surface and do not live in deep water beyond the reach of ground swells are liable to considerable pressure from the shifting of the loose material that surrounds them. Hence these generally have acquired stout, more or less globular shells as in *Isocardia* (Plate XXX., Fig. 9), the Cockle, *Cardium*,* the Veneridæ, etc.

The disadvantage of this form of shell, of course, is the amount of muscular power required to force a passage with it down into the sand. A gauge of this may be seen in the huge scar of the retractor pedis muscle in the Veneridæ, that has generally been

* It is interesting to note that the spines on the shell of the prickly species of *Cardium* are more pronounced on those dwelling in sand than on the individuals inhabiting muddy or silty sea-floors, the more shifting material demanding better means of anchorage.

overlooked because it is situated at the back of the broad hinge-plate.

In proportion, however, as the Bivalve seeks shelter from the strains of the shifting sand, either in quieter waters, or by burrowing deeper, so the shell in response tends to become less heavy and solid, and to assume a flatter shape, permitting of more rapid passage down into the silt. This is seen in the later date forms such as *Tellina*, *Psammobia* (Plate XV., Fig. 7) and *Scrobicularia*. The habit of burrowing deeper is of necessity accompanied by an increase in the length of the siphons to insure proper respiration, and this in turn results in the prolongation of the posterior portion of the test to house them, as well as the ultimate abandonment of the flattened form, till finally, in the deepest burrowers, the Myidæ (Plate XV., Fig. 4) and Solenidæ (Plate XXX., Fig. 8) the closed shell is frankly abandoned, and the valves, which no longer cover the whole animal, function solely as fenders against lateral pressure from the surrounding silt.

Facility in penetration is, probably, likewise the accountable cause of the elongate shape of the rock-boring representatives of several families of Pelecypods.

There are a few instances among the Bivalves in which the shell becomes internal (*i.e.*, invested by the mantle): *Chlamydoconcha*, which passes its life attached to the sheltered sides of rocks by its byssus;

Ephippodonta, which is commensal in the burrow of a species of Prawn (*Axinus*); *Scioberetia*, which is a parasite in the ambulacral zones of an incubating Echinoderm (*Tripylus*); and *Entovalva*, which is parasitic within *Synapta*.

No instance of a shell-less Bivalve has as yet been recorded. While, therefore, it is not so pronounced as in the case of the Gastropoda, there is still evidence of an increasing tendency in the Pelecypoda towards the reduction of the shell as one proceeds from the more primitive to the more specialized forms.

One feature in connection with the Bivalve Shell there is that distinctly shows a tendency to simplification, and that is the progressive reduction of the number of teeth in the hinge. The oldest forms, such as many of the Palæoconcha of Neumayr, the more archaic living forms (Nuculidæ, Arcidæ, etc.), and the embryo shells of many higher forms (Ostreidæ, Pteriidæ, Philobryidæ, Mytilidæ, etc.) exhibit a more or less rectilinear hinge-line with numerous small teeth (Taxodont). In the yet more advanced forms (*Condylocardia* and *Scioberetia*) this stage, present in the early embryo, is succeeded by the series of folds (characteristic of the young stages of the higher Pelecypods) that subsequently divide off into cardinal and lateral teeth, thus linking the Taxodont with the Heterodont and Desmodont types of hinge. In these last groups the hinge teeth pro-

gressively dwindle in number, till in the most specialized Septibranchs they are wanting altogether, as they are also, exceptionally, in other less advanced forms (e.g., *Anodonta*).

In dealing with the Cephalopoda it is essential to take into account the past history of the race, since so many, especially of the shell-bearing forms, have long been extinct.

The modern representatives of the class number close on 500 species, belonging to about 80 genera, of which total about half are referable to the genera *Polypus*, *Sepia*, and *Loligo*; while only 5 species (or less), all belonging to the genus *Nautilus*, are possessed of an external shell.

The Nautiloidea, which began in the Cambrian with seven straight-shelled species representing four genera, attained their maximum in the Silurian with about 230 species belonging to 20 different genera and subgenera. Since that epoch they have steadily diminished in numbers down to their minimum at the present day, while the surviving genus, *Nautilus*, only made its first appearance in the Trias, or in its present limited sense in the Tertiary. Nor did the vigorous offshoot of Ammonoidea that started in the Devonian and attained to a countless host of species, which from some monographs one might almost infer were referable to an equal number of genera, succeed in keeping up the number of testaceous Cephalopoda; for with

the close of the Cretaceous period the whole group died out after experimenting in every type of shell-form in the effort to survive.

Nothing is at present known of the embryonic development of *Nautilus*, and we do not, consequently, know if the primitive embryo shell differs in any respect from the adult; but the fact that the earliest Cephalopods had straight shells, and that the line of development led through curved to coiled forms is suggestive, and raises the speculation whether the primitive Gastropod shell may not also have been straight, and this phase in its development subsequently suppressed in its embryonic history.

Following up the scale of geological time, we meet with the first of the Decapods (*Aulacoceras*, belonging to the family Belemnoteuthidæ) in the Trias. It is interesting to note that, in the same series, the earliest Gastropod referable to the Tectibranchia, a species of *Bullinella*, is also recorded, so that we have a Cephalopod with an internal shell comparing in time with a Gastropod of a group that only subsequently in the Chalk period achieved a partially internal shell (*Philine*).

The Myopsida, or next higher tribe of Cephalopoda, began in the Lias (*Geoteuthis* and *Beloteuthis*), while in the Cretaceous of Lebanon the oldest known Octopod, *Palæoctopus Newboldi*, makes its appearance just as the Belemnites and Ammonites disappear from the scene.

So far as the shell is concerned, then, the Cephalopoda seem to have been yet more eager than the Gastropoda to jettison the encumbrance, and their predatory habits have obviously had much to do in hastening this consummation.

Turning next to the form of the animal itself, it cannot be said that any definite line of development is presented, unless, perhaps, in the case of the more specialized Gastropoda, where, with the discarding of the shell, the visceral hump tends to be smoothed down and distributed along the dorsal keel, till the true slug-like form is attained. Even this seems to be due to the burrowing habit of the animal rather than indicative of any definite product of development.

Allusion has already been made (*ante*, pp. 33, 34) to the great inequality of size the anterior and posterior portions of the body present in certain forms like *Mytilus*, and the disappearance *pari passu* of the anterior adductor muscle in proportion as, by the increase of growth in the posterior portion of the body, it is brought more and more into line with the hinge and posterior adductor muscle, and consequently ceases to be needful. It is possible that in the case of *Mytilus* the predisposing cause may be due to the long-continued action of gravity operating on successive generations of suspended animals, aided possibly by some other morphological tendency. Whether a similar tendency to monomyarianism observable in forms that like *Pecten*, *Ostrea*, etc., rest

on their sides, may be attributable to a like cause, is not clear, but it is at least remarkable that so many of the Monomyaria should be forms that assume a position out of the normal vertical.

Tridacna, so long a puzzle, and concerning which it was even held that the animal must have rotated in its shell, has been shown to be simply a case of a Monomyarian that has taken to live with its umbo downwards. All its anatomical features correspond closely in arrangement and position with those of *Mytilus*, only it occupies a relatively reverse position and its huge plastic body tends by its own weight to spread out, and consequently to form a shell that has its longer axis in a direction at right angles to that in the *Mytilus* shell.

Among other variations induced by environment is that of "dwarfing," which in every case appears, and naturally so, to be traceable to the prevalence of unfavourable conditions.

Thus there is a tendency in Land Snails to become stunted in size, as they attain to altitudes beyond those in which food is plentiful and other conditions of life most favourable to them. This is noticeable among forms dwelling in high valleys of the Alps, and is observable even in those on high hills in our own country. Indeed it is claimed that on Giltar Head, Tenby, which is 100 feet above sea-level, the specimens of *Helix Pisana* are dwarfed and stunted in comparison with those members of the

noted colony that dwell on the sand-hills just above high-water mark, which is the normal habitat of the species. On the other hand, the little black and white banded Snails (*Helicella virgata*), so common over our chalk downs, when they take up their abode among the sand-dunes by the sea, become dwarfed in their turn.

Marine coastal species will also show variation according to the favourable nature or the reverse of their surroundings.

Marine or freshwater species compelled to live in brackish-water conditions are very liable to dwarfing and distortion.

Freshwater Mussels (*Unio*, *Anodonta*) are readily affected by the quality of their surroundings, while Semper has shown by experiment that the volume of water allowed per individual has a very marked effect on specimens of *Limnæa stagnalis*, the size attained varying directly in proportion to the volume of water allowed.

The foot largely modifies in response to individual requirement, whether for locomotory or other purpose.

The Chitons and Gastropods creep about on the sole of this muscular organ, the action of which is best studied by observing a Snail crawling on a piece of glass (Plate XXXI.). The optical effect of the motion suggests a rapidly flowing stream proceeding from the tail towards the head, and this is due

to the successive raising, moving forward, and re-planting down of succeeding portions of the under surface of the foot, and is comparable to the mode of progression in a caterpillar, save that only the creeping surface and not the whole body participates in the action. The lateral margins frequently do not share in this motion, but have a gentle, lateral, undulating movement of their own.

Progressing in this way it has been calculated that an average-sized Snail of moderate pace travels at the rate of about a mile in sixteen days fourteen hours, while a Slug, having no "house" to carry, can cover the distance in eight days.

This mode of locomotion is assisted by the secretion, from glands in the foot, of mucus, which acts as a lubricant. The principal of these glands are situated at the front of the foot, in the middle of its under surface, and at its extremity. The mucus in many cases solidifies on contact with the air or water, as in the familiar shining track of the Snail. In certain of the Slugs it is sufficiently abundant and tenacious to permit of the animal utilizing a thread of it to climb from one leaf to another, or to descend from an elevated object, and even to reascend by climbing the filament thus formed. The Water Snails freely make use of mucous filaments to ascend to and descend from the surface to which they must resort for breathing purposes, and are probably also assisted by their mucous secretion when crawling in

an inverted position on the under side of the surface film of the water.

The float of the ocean-roving *Ianthina* (Plate XXX., Fig. 2) is another product of the pedal glands in which air bubbles are entangled with the mucus.

All Gastropods, however, do not glide onwards with the steady movement of the Snail. *Melampus* and *Pedipes* have the front portion of the foot ("propodium") marked off by a groove across the ventral face, and the animals, when crawling, first advance this propodium and then drag the rest after it. In the Periwinkle (*Littorina*) and some of the Pomatiidæ (= Cyclostomatidæ) the foot is cleft longitudinally, and the animal walks by lifting and advancing the alternate halves, like a man with his ankles tied together (Plate II., Fig. 5).

The propodium is strongly developed and reflected over the head in *Natica* (Plate II., Fig. 2), *Sigaretus*, *Oliva*, *Harpa*, and others that force their way through sand on the sea-bottom, and thus apparently acts after the manner of a snow-plough. The expansion of the foot in the Naticidæ is assisted by the presence of aquiferous spaces, which are completely separated from the circulatory apparatus.

In certain of the Rhachiglossa and some of the Opisthobranchs, on the other hand, the margins on either side of the lower surface of the foot (pleuropodia) are greatly extended (Plate II., Figs. 4, 6 and 8), and the animal is enabled to crawl on the

surface of the loose sand without sinking in, and to use them as fins for propelling itself through the water; while in *Notarchus* these two lobes are united above the body in such a manner as to form a muscular sac opening to the front, so that by forcibly expelling the contained water the animal can dart backwards.

The "wings" of the Sea-Butterflies (Pteropods) are a further modification of these pleuropodia (Plate XXVI., Figs. 1-16). In the Heteropoda the columellar muscle is extended through and beyond the true foot, and expanded into a large and laterally compressed fin (Plate XXVI., Fig. 20, *f*), which forms an efficient swimming organ as the animal progresses in an inverted position through the waters of the open sea.

The huge West Indian Fountain Shell (*Strombus*) uses its foot in quite a different fashion. The propodium is quite distinct, while the latter portion ("metapodium") is elongate and bears the claw-shaped operculum at its extremity. When the animal moves, it advances these two sections of its foot, thrusts them into the silt, and then using them as anchors, slides the heavy shell forward. Other Strombs (Plate VIII., Fig. 3) and their kindred *Pterocera* (the Scorpion Shells), *Rostellaria*, etc., progress by bending the foot under the shell and suddenly straightening it, thus leaping and rolling over and over.

In sedentary Gastropods like *Vermetus*, and in the parasite *Stylifer*, the foot becomes reduced and atrophied; while in the free-swimming *Phyllirrhoë* it no longer exists as a distinct organ.

The more primitive Pelecypoda, such as *Nucula*, with its kin, and *Trigonia* (Plate XXX., Fig. 7) have a flat under side to the foot with fringed margins, that can be used as a creeping disc. *Lassæa* and *Sphærium* (Plate XVIII., Fig. 16), though they have no creeping disc, can also crawl on submerged objects, and some of them even on the surface film of the water. Most of the Pelecypoda, however, and the Scaphopoda, make use of the foot to force a way through the mud and silt in which they live. The foot is first extended in the direction in which the animal wishes to go, the blood is then forced into it so that it swells out and gives some hold on the surrounding silt, when by contraction of the pedal muscle the shell is hauled towards it. By a constant repetition of this process the creature slowly advances. The same method is adopted by those Bivalves, like *Mya*, *Solen*, etc., that live head downwards in sand. The Solens (*Ensis*, Plate XXX., Fig. 8, etc.), indeed, owing to the powerful development of the foot and elongate cylindrical shape of the body and shell, can bore down with such great rapidity that if the animal has been alarmed it is impossible to overtake them by digging. The foot of the Cockles not only serves them as a burrowing

but also as a leaping organ, and it subserves similar ends in *Trigonia*, *Donax*, and a few others.

In the case of those Bivalves that are inactive or stationary like the borers (*Pholas*, *Saxicava*, *Teredo*, etc.), or are attached, like the Oysters, some of the Scallops, etc., the foot becomes rudimentary through disuse; indeed, in the adult Oyster it is entirely wanting.

Certain of the Scallops dart about by rapidly opening and closing their valves; *Ensis* and *Solenomya* by expelling water from the posterior aperture of the mantle and siphons.

Of the movements of the little pelagic *Planktonmya* nothing is at present known.

While *Nautilus* creeps about on its numerous series of weak tentacles, the Cuttlefish crawl about and catch their prey by means of their far more powerful arms. Some of the latter swim leisurely through the water by means of their fins; but all, including *Nautilus*, can dart rapidly backwards by expelling the water from the pallial cavity through the funnel.

Among the evolutionary developments called forth by environmental requirements may be reckoned those instances of protective resemblances and coloration that are as prevalent in the Mollusca as in the rest of the animal kingdom.

The mottled markings on the shell of the common Garden Snail play on a small scale the same part that they do in the Giraffe, and serve to make the

wearer less conspicuous in the shadow of vegetation. The dun colour of the Desert Snail (*Helix desertorum*), like that of the other desert animals, harmonizes with the prevailing tint of the habitat. The arboreal *Ariophanta Dohertyi* of Sumatra is of a delicate green colour, and almost invisible amongst the foliage on which it dwells. Many of the Slugs, by their colouring and markings, are rendered inconspicuous in their natural surroundings, such as *Limax arborum* on trees, *Geomalacus* (the Kerry Slug) on lichen-covered rocks. Certain of the Philippine genus *Helicostyla* carry colour protection to a higher stage: when dry their grey-brown periostracum, which is full of air spaces, matches in colour the dead foliage of the forests where these Snails have their abode; when the heavy showers, which are frequent, impart a rich dark colour to the dead leaves, these air spaces are filled up by the moisture, and their periostracum then allows the underlying dark colour of the true test to show through, so that the shell once more harmonizes with its surroundings. On drying again it speedily resumes its former hue.

The reason for the coloration on some shells—Cones, for instance—that are covered during life with a thick periostracum is not readily explicable.

Many of the marine shells, however, that are not thus invested, are so marked as to be inconspicuous in their proper habitat; while others are coloured to match the objects on which they live or prey.

Thus *Ovula* and *Pedicularia* are yellow or red according to the colour of the corals on which they occur.

The phenomenon is common enough among the Nudibranchs. Green specimens of *Hermæa dendritica* confine themselves to green seaweeds, whereas the red *H. bifida* is found only on red weeds. *Archidoris flammea* closely assimilates in hue the bright red sponges on which it feeds. Endless similar instances are, in fact, afforded by this group.

Pelagic species of Mollusca are generally transparent and colourless, unless tinged with blue.

Protective coloration is, however, carried to its greatest perfection in the Dibranchiate Cuttlefishes. Scattered over the skin of these animals are pigment cells containing different colours which become visible on the expansion of the cell by the muscle fibres with which each is furnished. Their control is connected with the visual nerves, and by reflex action they are brought into play, so that the creature is able more or less voluntarily to adapt the colour of its body to its immediate surroundings after the more familiar example of the Chamæleon.

More frequently, perhaps, protection is as it were adventitiously afforded by the shell becoming coated over with extraneous matter. Many of the land shells, especially those living among the roots of plants, tend to become coated over with earth. *Limnæa truncatula*, which delights to crawl out of water on wet mud, is usually so coated over as to

resemble a small mass of that substance. The shells of the true Water Snails are often quite overgrown with minute green weed, and so, too, are those of marine Gastropods. The latter, moreover, are frequently encrusted with calcareous Algæ (Nulipores, etc.), or overgrown with some Hydractinian till they are unrecognizable. A more curious and striking instance is offered by the genus *Xenophora*, the members of which build on to the upper surface of the shell, especially at its margin, fragments of stone, coral, or other shells—whatever, in fact, is common on the sea-floor where they happen to be, after the well-known manner of the Caddis-worm (Plate XXVIII., Fig. 3).

Among the Bivalves some species of *Lima* and *Volsella* (= *Modiolus*) attach various bits of marine refuse to themselves by threads of the byssus till they are more or less concealed thereby. *Lima hians*, indeed, is credited with a regular "nest" of this sort.

Of other forms of protection of a more active nature may be mentioned the possible advantage of spiny shells in preventing the occupant from being swallowed for food: the poisonous bite of the Cones may likewise serve in good stead.

It is among the more defenceless Opisthobranchs, however, that the best instances have so far been met with.

Oscanius is known to secrete an acid from the surface of the body. *Ancula*, *Doto*, and many of the

Æolididæ have stinging cells, like those of the Jelly-fish and Anemones, at the tips of their cerata. These creatures are conspicuously marked with what may be warning colours, and do not seek concealment.

Of mimicry proper, in which an animal seeks to resemble some surrounding object or some other and distasteful congener, some instances are met with among the Mollusca, and others will doubtless be forthcoming with more careful observation.

It has been suggested that some of the Land Snails, like *Clausilia* and certain of the Pupillidæ (=Pupidæ), as well as some Slugs, may derive a certain amount of protection from their passing resemblance to the fallen leaf-bud scales of trees, while some *Helices* closely simulate the seed-pods of the plants which they frequent. One of our Common Shore Periwinkles (*Littorina obtusata*) is thought to resemble the air bladders on the seaweed (*Fucus*), among which it dwells. *Lamellaria perspicua*, a tænioglossate mollusc with internal shell lives on Ascidians, and in coloration and markings accurately reproduces the appearance of the colonies of its victims. Conspicuously coloured Nudibranchs like *Doto coronata* and *Dendronotus frondosus* closely resemble colonies of Hydroids among which they dwell. *Jorunna Johnstoni* lives associated with a sponge (*Halichondria panicea*), for the little colonies of which it is readily mistaken. Now, Hydroids have stinging cells, and the Ascidian in question, as

well as the sponges, needle-like spicules which make them undesirable as articles of food; hence the importance of the mimicry.

How far one mollusc devoid of special self-defence may mimic another kind furnished with some defensive protection is a moot point. It has been suggested that a certain species of *Strombus*, the shape of whose shell resembles that of a *Conus*, may derive some advantage thereby in view of the poisonous bite of the latter.

There seems more probability in the case of two Philippine Land Snails—*Helicarion tigrinus* and *Xesta Cumingii*—both possessed of a small thin shell, into which the animal cannot retire, and a remarkably long, narrow, high-ridged "tail" to the foot, which forms the most likely looking hand-hold for their capture. When so seized the *Helicarion* parts with its tail and escapes, while the *Xesta* is unable to do so, and it is thought that birds acquainted with the futility of attempting to capture the one would leave the other in peace also.

The alimentary system in its entirety does not present features of evolutionary interest, although minor variations in response to individual requirements are numerous. Of these the most interesting is the development in the gizzard of the Bullidæ of calcareous plates (Plate III., Figs. 9 and 10), whose function is to crush the small shellfish, which are swallowed entire.

The radula (Plate III., Figs. 11-22), which is characteristic of the phylum, exhibits consistent progress as one passes from the lower to the higher groups. In the older families, especially the *Rhipidoglossa*, the teeth are weak, but numerous; indeed, there may be as many as 300 or more in each transverse row. The most archaic member of the group, *Pleurotomaria*, shows the most primitive type and indicates that it has been derived from an earlier one, in which all the teeth in a transverse row were similar. Now, in *Pleurotomaria* and the more primitive *Rhipidoglossa*, three longitudinal tracts on either side of the median tooth are distinguishable, but in the higher members of this division it is found that the several teeth in one tract are replaced by a single large one, which generally retains sufficient traces of the individuals it replaces to suggest that it represents the fusion of a series. Similar cases also occur in molluscs yet higher in the scale. This fusion, extending to all the tracts, results in the tænioglossate radula, whose formula is 1 : 1 : 1 : 1 : 1 : 1 : 1 (or 2 : 1 : 1 : 1 : 2, Plate III., Fig. 15). By further fusion, or, rather, as would seem to be more probably the case, by the abortion of the outer rows of laterals, is derived the type of radula met with in the *Rhachiglossa* and more primitive of the *Toxoglossa*, whose formula is 1 : 1 : 1 (Plate III., Fig. 17). In *Harpa*, *Marginella*, and the *Volutidæ* (Plate III., Fig. 18) the process is carried a step further, and only the

median tooth is left. In the Cones (Plate III., Fig. 19), on the other hand, it is the median row that disappears, leaving the double row of barbed laterals. Of course this line of development is not exemplified in all. Numerous cases of apparent exception occur among families that lie off the main branch, or that in this respect retain archaic characters. Such are *Epitonium* (Plate III., Fig. 14), *Ianthina*, etc.

The Opisthobranchia offer every variety of radula in their ranks from the uniform multiserial to the single row of median teeth in *Elysia*, and much further research will be necessary ere a solution of this diversity is found.

The Pulmonata branched off early, and have retained a primitive form of radula, such modifications as there are being principally in the number and form of the cusps on the individual teeth (Plate III., Fig. 21). These modifications proceed from the median line outwards, so that an inspection of the marginal teeth, or those of the embryo, gives a clue in many cases to the ancestral radula. Only one genus, *Polita*, shows an appreciable diminution in the number of teeth, for whereas the Common Garden Snail (*Helix aspersa*) has about fifty-five teeth on either side of the median in each transverse row, this number is reduced in *Polita* to at times as few as twelve.

The higher Cephalopoda (Plate III., Fig. 20) have

fewer and more powerful teeth than *Nautilus*. The latter has four teeth on either side of the median, with basal plates representing two others, whilst the rest have three on either side, sometimes flanked outside with a single basal plate, while in one genus only, *Gonatus*, but two laterals are left on either side.

The circulatory system can be adduced as showing development if those of the tribe at the head of the phylum (the Dibranchiate Cephalopods) and of the primitive Gastropods be contrasted; for in the latter the circulatory system, instead of branching off into capillaries, is distended into swollen, irregular cavities and sinuses, which are, so to speak, insinuated among the various organs of the body, while a certain amount of the blood finds its way back to the heart without passing through the respiratory organs. The Dibranchia, on the other hand, have the most complete circulatory system of any mollusc, the blood being nearly entirely contained in true vessels.

The molluscan heart, at the same time, offers some anomalies when the different groups are compared. It is most primitive, and more nearly approximates the annelidean type, in *Nautilus*, where the single ventricle (and no mollusc has more than one) is served by four auricles, whereas in all the other symmetrical Mollusca it has but two auricles (except in the Scaphopoda and Aplacophora, in which the heart is rudimentary).

In the streptoneurous Gastropoda, proportionately

as the right (originally left) ctenidium becomes aborted in the higher Rhipidoglossa, and disappears in the rest, as the result of the general torsion of the body, so the corresponding auricle diminishes and disappears also. The simplification of the heart in this case, therefore, is not due to any progressive development from a less to a more perfect condition.

The respiratory system supplies some very interesting points. There is every indication that the primitive gill of the Mollusca must have consisted of at least a pair of very simple plume-like structures, and that as increased facilities for respiration were required, which, of course, implied increase of gill-surface, it could only be obtained in one of two ways: the flattening out into a leaf-like expansion of the individual gill-filaments (aspidobranch), or their prolongation (pectinibranch). The former modification is the one that appears in all the archaic members of the different classes, and may be recognized in the Polyplacophora, the rhipidoglossate Gastropoda, the protobranchiate Pelecypoda, and in the Cephalopoda. This structure, nevertheless, is limited by the confined space of the pallial cavity, and further increase of surface can only be gained by the corrugation of the gill-filament. A beginning of such plication is observable in the case of *Pleurotomaria*, and doubtless it exists in other Aspidobranchs as well; but it is carried to a much greater degree in the Cephalopoda, in which the gill-fila-

ments exhibit two series of plications crossing one another.

In the Gastropoda the progressive atrophy and disappearance of the right (originally left) ctenidium as one ascends from lower to higher members has already been alluded to (*ante*, p. 24). The initial stage of this is shown in *Pleurotomaria*, but it is far more marked in *Scissurella*. In the Pectinibranchia not only has one ctenidium disappeared, but the other (except in the case of *Valvata*) has become attached by its whole length to the wall of the pallial cavity, and as a consequence has parted with the whole of the row of filaments on that side; so that three-quarters of the gill-potentiality of the primitive mollusc is sacrificed. By way of partial compensation the individual gill-filaments have been somewhat lengthened till the familiar pectinibranch condition arises. In *Ianthina* (Plate XXX., Fig. 2) these gill-filaments are furthermore plicated.

The complicated modifications that take place in the gills of the Pelecypoda have already been described (*ante*, pp. 28 and 29), since the classification of the group is based thereon, and need not be redescribed.

Many kinds of aquatic molluscs have lost their gills altogether, and in these cases the respiratory function is taken up by the mantle. This is the case with the Common Limpet (Plate IX., Fig. 7); the circle of "gills" surrounding the edge of the mantle just under the shell are outgrowths of the

mantle. So, too, are the plume-like gills of many of the Nudibranchs (Plate XII., Fig. 20-28), but in others of this group those curious outgrowths known as "cerata," as well as the general mantle surface, also take on the function of respiratory organs.

In the terrestrial Snails and freshwater Pulmonates respiration is carried on by means of the complex network of blood-vessels that overspread the roof of the pallial cavity, which thus acts as a "lung." In one family of marsh-frequenting Snails (*Ampullariidæ*) the pallial chamber is divided into two, the right-hand containing a gill, while the left is converted into a pulmonary chamber, whose opening is transformed into an extrusible siphon which the animal uses if near the surface of the water; or it can breathe by its gill under water and by its lung when out of water (Plate II., Fig. 1).

All these changes appear to be made in response to the demands of the environment, even the highly complicated structure evolved in the Pelecypoda is a question of the requirements of respiration solely. The majority of the gill-bearing Gastropoda and the less specialized Pelecypoda live in waters that are constantly in a state of more or less agitation, and where, consequently, entangled oxygen is comparatively abundant; whereas the Bivalves that burrow do not get the water in their lurking-places so fully or so frequently aerated, and hence the necessity for being able to extract proportionately more oxygen

from the water around them, and the consequent development of the gill in response to this demand.

The fact, for instance, that *Anodonta* has developed such a complicated gill-structure becomes intelligible when it is borne in mind that it lives mostly in ponds or sluggish water, and has, moreover, for six or eight months out of the twelve to shelter within its gill-chamber hundreds of young, all like itself consuming oxygen from the same limited supply.

In the nervous system of the Mollusca (Plate III., Fig. 3) a definite progressive development is traceable. In the earlier and more archaic Gastropoda the nervous system is diffuse, the nerve ganglions are comparatively widely separated, and the connectives and commissures that unite them are long. Passing to higher and higher representatives, the nerve centres tend to become more and more concentrated; at first the sensory and motor nerve centres, and then all the others, till they form a ring round the anterior part of the œsophagus, and finally are intimately united and localized on the dorsal surface of the latter, as in *Pleurobranchus*, or the ventral side, as in the thecosomatous Pteropods. This progressive advance is observable also in the Cephalopoda, and to a lesser degree in the Pelecypoda, and even the Amphineura.

Of the sensory organs, only the eyes call for mention. With the exception of the Cephalopods, and possibly the Heteropods, the vision of the

Mollusca is limited. The Cephalopods and Gastropods afford instances of progressive development in this organ. In *Nautilus* and in the Limpet the eyes are simple pigmented infoldings of the integument without any refractive body (Plate XXIX., Fig. 12, C). A crystalline lens is present in the more archaic rhipidoglossate Gastropods, and in the rest of the Gastropoda this is enclosed by a cornea (Plate XXIX., Fig. 12, B). A cornea—incomplete in the Oigopsida (Plate XXIX., Fig. 12, A), but complete in the Myopsida—is also present in the dibranchiate Cephalopoda, while the Octopus, in addition, possesses an eyelid. In those cases in which the eye becomes buried in the integuments, or the animal is abyssal or subterranean in habitat, this organ tends to become rudimentary (certain Naticidæ, Bullidæ, the Pleurobranchidæ, and some Pulmonates) or to be wholly wanting (sundry species of *Natica*, *Terebra*, of the Olividæ, *Bullia*, some subterranean Pulmonates, certain abyssal Gastropods, internal parasites like the Entoconchidæ, and pelagic forms such as *Ianthina* and the Pteropods).

Among the Bivalves, except the Mytilidæ and *Pteria*, true cephalic eyes are wanting in the adult, though present in some larvæ.

Accessory eyes are developed in some molluscs in other parts of the body. In certain species of *Chiton* scattered over the shell are many thousands of eyes, some with and some without crystalline lenses ; they

are ranged in rows running from the front beak of each shelly plate diagonally to its outer edge. Some species of the pulmonate *Oncidium* have, in addition to the eyes on the tentacles, a large number of others situated on tubercles over the back. These particular Slugs are said only to be found in the mangrove swamps where the peculiar fish *Periophthalmus* abounds, hopping along the shore in search of prey, and it has been suggested that there may be some connection between these two occurrences, but nothing very definite has been decided.

In certain of the Pelecypoda accessory eyes are found on the edges of the mantle and at the extremities of the siphons. In the Arcidæ there are compound eyes to the number of more than two hundred placed along the mantle margin. *Pecten* (Plate XV., Fig. 8) and *Spondylus* have nearly as many, but they are isolated and borne each on a short tentacle, more being found on the margin of the left, or upper, than on that of the right, or lower, mantle lobe. The structure of these accessory eyes in *Oncidium* and the Pectenacea resembles the vertebrate eye in that the visual rods are turned away from the light. Less complex visual organs, but nearly equally sensitive to light, are found in the mantle margin of *Ostrea*, *Pteria*, *Pinna*, and *Mactra*. The tentacles at the ends of the siphons of *Cardium* (Plate XXIX., Fig. 13), *Lithodomus*, *Pholas*, *Mya*, *Ensis*, and others, bear eyes that are more or less sensitive to light and

shade, and so warn their possessors of the approach of possible danger.

With all this capacity for ready response to the action of environment, it is little wonder that members of widely different families and even orders, subjected to similar conditions of existence, should come to bear striking resemblance to one another. To the recurrence of the Limpet-shaped shell and the repetition of the Slug-like form, allusion has already been made (*ante*, pp. 103 and 106). Many other similar instances occur among Gastropods, notably *Sycotypus* (Rhipidoglossa), which resembles *Ficus* (Tænioglossa) Plate XXXII., Figs. 11 and 12), and *Strombus Mauritanus* (Tænioglossa), simulating *Conus Janus* (Toxoglossa), while there are equally noteworthy examples among the Pelecypoda. *Coralliophaga*, a genus of Cyprinidæ (Eulamellibranchia), in its external appearance closely resembles *Lithodomus*, one of the Mytilidæ (Filibranchia) (Plate XXXII., Figs. 17 and 18), whose burrows it occupies (*ante*, p. 54). *Dreissensia*, the freshwater Zebra Mussel, belonging to the Submytilacea (Eulamellibranchia), is constantly misplaced on account of its striking similarity to *Septifer* with the Mytilacea (Filibranchia) (Plate XXXII., Figs. 13 and 14). Another noteworthy instance is that afforded by *Petricola pholadiformis*, one of the Veneridæ, recently introduced into this country, seemingly with Oysters from America, that at first

glance is remarkably like *Barnea* (Pholadida), and occurs in similar situations (Plate XXXII., Figs. 15 and 16).

The reproduction of lost parts takes place to a considerable extent among the Mollusca. Experiments made in the eighteenth century by Spallanzani, and fully confirmed later by Tarenne, go to show that Snails can reproduce not only the tentacles, but even at times the whole head, while Madame Power obtained similar results so far as portions of the foot, mantle, and tentacles of marine species were concerned. The cerata of Nudibranchs it is known can be reproduced, as well as the arms of Cuttlefish and the siphons of *Ensis* and *Solecurtus*. In some cases self-amputation can be voluntarily performed and the parts reproduced. This is the case with the swimming lobes of *Lobiger*, the hind-portion of the foot of *Harpa*, and the long mantle fringes of *Lima*. These last will live for some hours after separation from the animal. The phenomenon has also been observed among Land Snails. Thus in Cuba, Gundlach has recorded that *Pleurodonta imperator* and *P. crassilabris* part with the hind-portion of the foot, which will show signs of animation fifty-four hours after, the line of separation always occurring at the same spot, and the lost part being soon reproduced. The West Indian *Stenopus* is credited with a like faculty. In the Philippines, Semper

records finding a species of *Helicarion* (already alluded to, *ante*, p. 124) that shed the "tail" when touched by whisking it up and down till it became detached, or if seized by the "tail" the animal dropped off and escaped.

CHAPTER VIII

INSTINCT, INTELLIGENCE, AND USES

INSTINCT and intelligence as we understand them are hardly qualities that one would look for in molluscs, nevertheless the homing instinct is displayed by more than one. The Limpet is well known to return after each grazing excursion to the selfsame spot on the rocks to which it has fitted its shell. The Common Garden Snail and the Slugs punctually return after each nocturnal ramble to the nook or corner, crack or cranny that each has made its home. A somewhat higher order of intelligence is that cited by Darwin on the authority of Mr. Lonsdale, in which a Roman Snail (*Helix pomatia*) made its way from an ill-stocked garden over the wall to one rich in plant-life, and returning, fetched a weakly companion, which it piloted to the land of plenty it had discovered.

Madame Power declares that she once saw an Octopus in her aquarium watch a *Pinna* till the shell was well open and then deliberately place a fragment

of rock, which it held ready, between the valves to prevent them closing, when it easily devoured its defenceless victim. The same animal was also seen to watch by the side of a big Gastropod till the latter emerged from its shell, when the Octopus pounced on it.

The uses to which Mollusca and their shells both have been and are put seem almost endless. Primarily they have served from prehistoric times as articles of diet. The shells of Oysters, Mussels, Cockles, Periwinkles, and other edible kinds, mixed with bones of beasts and birds that had shared their fate, are found in the refuse-mounds known as "kitchen - middens," which range from 100 to 1,000 feet in length, and from 3 to 10 feet high, and which occur along the coasts of Denmark, and are even represented by small deposits in places in these islands. Later-date counterparts of these refuse-heaps are met with in North America, formed principally of the valves of *Venus mercenaria*, in Brazil, Tierra del Fuego, Australia, New Zealand, etc. In caverns in Liguria enormous accumulations of Limpet shells tell a like dietary tale.

To-day nearly all the marine Bivalves are eaten in one quarter of the world or another, as well as many of the marine Gastropods and even Chitons. Cuttle-fish are esteemed in Italy, Provence, Spain, China, Japan, and the East generally.

The freshwater molluscs, being less tasty, are not

so much resorted to, but they have some adherents among the natives of Mauritius, Guadeloupe, and Cambodia; even in France some of the freshwater Mussels are eaten in certain localities.

Land Snails have been consumed from very early times. The yellow-banded Snail (*Helix nemoralis*) figures in the kitchen-middens, and the Romans, who were great snail-eaters, most probably inherited, and did not initiate the custom. In France great quantities of the larger Snails are eaten, and formerly certain annual Snail feasts were held in the North of England. Different kinds furnish repasts in various parts of the world.

How far molluscs may have been cultivated for food in very early days cannot now be guessed, but in Roman times a certain Sergius Orata, about 100 B.C., established vivaria for Oysters on the Lucrine Lake, near Baiæ, and obtained much notoriety for his produce. To-day Oyster farms are abundant in France, England, and the United States. To the Romans are also due the first "cochlearia," or Snail farms, invented by Fulvius Herpinus, and in Central France, where the animal no longer lives, masses of the shells of the Roman Snail (*Helix pomatia*) mark the former sites of such. Similar farms are in use on the continent at the present day.

Mollusca are further very largely used as bait in fishing. Slugs and Snails have also figured copiously

in the Pharmacopœia from Pliny's days, and down to quite recent times there has been a widely prevalent belief that they were especially efficacious as a remedy for consumption.

After food comes ornament. In various caverns of the Stone Age in Southern France numbers of littoral shells bored for the purpose of threading have been found, as well as fossil shells similarly treated. Present-day savages in all parts of the world utilize them for personal adornment in many ways, sometimes simply boring and stringing them, sometimes preparing portions only by rubbing down till the required part is left. Specially prized kinds are either employed for particular forms of ornament or are reserved for the exclusive use of chiefs. Sections of big Top Shells and Cones forming large rings are prepared and used as bracelets, and recently were imported in quantities as armlets for ladies to keep up the long gloves then in fashion.

Their other modern uses for ornamental purposes, as well known, are extensive and varied—from ash trays to Mother-of-Pearl inlaying work, while pearls form an additional item apart, and have been highly esteemed from very early times. These are obtained not only from the Pearl Oyster of Ceylon and the East, but are met with in the freshwater Pearl Mussel (*Margaritana margaritifera*), and their fishing once formed a valuable industry; while the occurrence of pearls in the Zebra Mussel (*Dreissensia*) in

Staffordshire has been recorded. Indeed, the Romans seem to have held the British freshwater Pearls in high estimation; while, according to Pliny, Cæsar dedicated to Venus Genetrix, and hung in her temple at Rome, a breastplate covered with British pearls, though these were possibly from the marine Mussel, which, as well as the Oyster, sometimes yields pearls. A large dull kind of pearl is also got from *Tridacna* (the Giant Clam), and pink Pearls from the West Indian Fountain Shell (*Strombus gigas*), as well as from certain *Turbinella*. Fossil pearls of large size have, moreover, been found in our English chalk, being the product of the big Bivalve (*Inoceramus*) that occurs therein. Dr. Willey was fortunate enough to obtain a large pearl from a *Nautilus* shell in New Britain, this being apparently the only one known.

For practical utilitarian purposes, however, the South Sea islanders make the most use of shells. They employ them as sinkers for their fishing nets in some cases as bait for Cuttlefish, manufacture fish-hooks, weapons, and even shaving tools out of them.

In China and Japan the translucent shells of *Placuna placenta* are used for windows, and there is a "Window-Shell" Oyster fishery near Trincomalee, Ceylon.

The silky byssus of *Pinna* has been woven into gloves, caps, stockings, etc., and Taranto, in South

Italy, was the headquarters of this quondam industry.

In some quarters of the globe shells serve the purpose of money. Of these the best known is the Money Cowry (*Cypræa moneta*), which used to pass for currency in India, and is still largely used in West Africa. Among the tribes of North-Western America a species of *Dentalium* was employed till superseded by blankets. On the eastern coast of North America, "wampum" was long the medium of exchange: it was formed of beads made by grinding down the Common Clam (*Venus mercenaria*). Another form of wampum, made from *Saxidomus* and *Haliotis*, was current in California, while in Benguella the same sort of money was manufactured out of a Land Snail (*Achatina monetaria*).

In New Britain the native shell-money, or "diwara," consists of shells of *Nassa callosa*, bleached, perforated by knocking off the curious hump, and threading them on rattan slips.

Besides these there is the shell-bead-money, generally known as "rongo," of Malaita, in the Solomon Islands, which is of three colours—white, red, and black. The white is made from *Arca granosa*, the red from *Chama Pacifica*, and the black from a black Mussel, or *Pinna*.

More quaint was the custom prevalent at one time on the west coast of Scotland, whereby, when a bargain was struck, each of the parties kept one-half

of a Bivalve shell, the vendor receiving back the counterpart on the completion of the transaction by way of receipt.

In agriculture shells were formerly much used in districts where lime was scarce for dressing the soil, and also, it has been stated, in the manufacture of porcelain, but for this there appears no warranty.

Dyes have been extracted from molluscs. The Tyrian purple of the ancients was obtained from certain species of *Murex*. *Aplysia*, the Sea-Hare, yields a violet fluid; so, too, does *Ianthina*, and an indelible dye is obtainable from the common *Purpura* of our coasts, but no practical use appears to have been made of them.

As some measure of the part shells play in commerce it may be mentioned that in 1910 £587,115 worth of shells of all kinds were imported into this country, nearly one quarter being from Western Australia.

While, however, man has thus profited by the mollusc, the latter, at times directly, but more frequently indirectly, has its revenge. More than one diver and bather has suffered from the embrace of the Octopus and supplied sensational material for the fiction writer. The Cones are capable of inflicting a poisonous bite on the hand of the unwary captor. The Oyster and Cockle from sewage contaminated beds, immune themselves, will convey the germs of typhus to the consumer, while Mussels are

frequently the cause of poisoning when eaten. *Limnæa truncatula*, as already stated (*ante*, p. 79), is the intermediate host of the Liver Fluke of Sheep.

The mischief that Slugs and Snails can work to crops and in gardens is only too well known; the former are also said to damage corks.

The amount of mischief that has been caused by the Ship-worm (*Teredo*) is almost incalculable, but with the passing of the wooden ship and the extensive use of iron and steel work for piers, its destructive energies are now mainly confined to the timber work of groynes and landing-stages. There it is still the despair of the engineer, for no known method of treating the piles will keep the foe at bay.

The prices paid by collectors for fine specimens of rare shells, although at one time considered high, are insignificant beside those given of late years for scarce postage stamps. Thus £43 10s. was paid in 1854 for a *Conus gloriæmaris*, and £42 in 1865 for another example. The latter figure was also realized the following year for a specimen of *Cypræa guttata*, and £40 for a *C. princeps*, while as much as £100 is said to have been given for a single specimen of the heteropod *Carinaria*, now worth only from £5 to £10. Of late years the highest sum paid for a single shell was that given for the magnificent *Pleurotomaria Adansoniana*, now in the Natural History Museum, for which the original vendor obtained £55.

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